FORAGE FISH AS A PREDATOR: SUMMER AND FALL DIET OF ATLANTIC HERRING IN TRINITY BAY, NEWFOUNDLAND

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Abstract

Atlantic herring (*Clupea harengus*) is an important forage fish in the Northwest Atlantic. However, the diet of herring in eastern Newfoundland is unknown. I compared plankton assemblages to stomach content and stable isotope analyses of Trinity Bay adult herring collected in the late summer and fall (2017-2019) to characterize diet and selectivity. Amphipods (*Themisto* spp.) contributed most to herring diets in 2017 and August 2018, while calanoid copepods dominated the diet in late 2018 and 2019. Fish eggs and larvae were consistently observed in stomach contents and were most prevalent in the diet when peak larval densities were observed. Stable isotope analyses found that herring fed on prey at a higher trophic level than zooplankton, supporting the importance of piscivory in adult herring diets. As an adaptive predator, Newfoundland herring are resilient to bottom-up changes and may also exert top-down pressure on the early life stages of other fishes.

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I also thank Dr. Robin Anderson and Bob Whalen (DFO) for sharing their expertise in stable isotopes and for the considerable time and energy dedicated to training my technicians in stable isotope processing. I acknowledge the support of three undergraduate technicians, Sean Comeau and Jennifer Blundon, who assisted with the preparation of all

stable isotope samples, and Ashley Pardy, for her assistance sorting herring stomach contents for identification.

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This study met all animal care requirements and was approved by Fisheries and Ocean Canada's Animal Care Committee (protocol number 2017-07).

Table of Contents

List of Tables

List of Figures

List of Abbreviations and Symbols

Abbreviation / Symbol	Definition
LRP	Limit Reference Point
LC	Labrador Current
CTD	Conductivity-temperature-depth
SE	Standard error
SIMPER	Similarity percentage analysis
DistLM	distance-based linear model
PERMANOVA	permutational multivariate analysis of variance
TL	Total length
PFI	Partial fullness index
TFI	Total fullness index
δ	Difference between stable isotope sample and standard
‰	Parts per thousand
NAOI	North Atlantic Oscillation Index

List of Appendices

Co-authorship statement

I primarily conducted the work completed in this thesis with the support of my co-advisers, Drs. Hannah Murphy and Maxime Geoffroy, as well as my committee member Dr. Dominique Robert. The body of this thesis presents a three-year field study exploring the diet of herring in Trinity Bay Newfoundland. Chapter II was prepared as a stand-alone document with the intent to submit for peer-reviewed publication in *Fisheries Research*.

The thesis includes data that were collected a year before I began a Masters in Science, so my involvement in fieldwork and lab work began in 2018. Dr. Hannah Murphy conducted herring collections in 2017 with support from the Pelagics team at Fisheries and Oceans Canada (DFO). I primarily completed the fieldwork in 2018 and 2019 with support from Dr. Hannah Murphy as well as the DFO Pelagics team. Ichthyoplankton samples in all three years were collected and all fish larvae were identified by Dr. Hannah Murphy and the DFO Pelagics Team. Dr. Dominique Robert and the technicians in his lab at Université du Quebec à Rimouski sorted and identified zooplankton samples for prey field analysis. Meredith Terry conducted herring stomach content analyses in 2017. I conducted a substantial portion of the stomach content analyses in 2018 and 2019 with help from Meredith Terry. All stable isotope preparations were done by undergraduate technicians hired for this purpose, with funding I secured in both 2018 and 2019. I conducted all the statistical analyses and manuscript preparation for the thesis with editorial support from my full committee.

Chapter 1: Introduction and Overview

1.1 Food webs and forage fishes

Food web dynamics are a crucial tenet of ecology, connecting all trophic levels of an ecosystem through the movement of energy (Lindeman 1942; Layman et al. 2015). The structure of food webs, such as the length of food chains and functional groups, serve as an essential tool to help understand how species interact both with each other and with their environment and have recently been incorporated into ecosystem-based models (Christensen and Walters 2004; Tam et al. 2017; Lam et al. 2019). In marine ecosystems, food chains typically only consist of three to four trophic levels (Rice 1995; Vander Zanden and Fetzer 2007) in which changes are primarily facilitated through two control mechanisms: top-down and bottom-up (Frank et al. 2007; Wollrab et al. 2012). Top-down control occurs when higher trophic levels influence lower trophic levels through processes such as predation, whereas bottom-up control occurs when lower trophic level organisms drive changes in the higher trophic levels, through processes such as nutrient availability (Power 1992; Frank et al. 2007; O'Connor et al. 2009). Forage fishes occupy a central role in marine food webs by acting as an energy conduit between upper and lower trophic levels and thus serve as a link between these two mechanisms (Lynam et al. 2017).

Generally, food webs are structured as trophic pyramids, with numerous taxa, including primary producers, at the lowest trophic level with progressively fewer predator taxa at higher trophic levels (Byrnes et al. 2007; Nagelkerken et al. 2020). However, some food

webs are dominated by one or two prey species at an intermediary trophic level (e.g., forage fishes) that serve as the main channel for energy flow from the lower trophic levels to top predators; these types of food webs are referred to as 'wasp-waist' ecosystems (Rice 1995; Cury 2000; Smith et al. 2011). Subsequently, changes in the abundance of species at the 'waist' of an ecosystem can disproportionately affect higher trophic levels by bottom-up control or release the lower trophic levels from predation (top-down control).

Forage fishes are small, slender-bodied fishes that represent a diverse range of families, including clupeoids (herring, shad, sardines, anchovies), osmerids (smelts, capelin), and ammodytids (sand lances). These taxa are also characterized by boom-bust population cycles that oscillate between periods of extreme high and low abundance (Lasker and MacCall 1982; Trochta et al. 2020). Some of the most well-known examples of forage fish population collapse following periods of immense productivity include the sardines in the California Current (Lindegren et al. 2013), the Peruvian anchoveta (Alheit and Niquen 2004) and the North Sea herring (Simmonds 2007; Dickey-Collas et al. 2010). Numerous studies have examined the environmental and biological factors that influence these dramatic changes in abundance (e.g., Lluch-Belda et al. 1989; Fréon et al. 2005; Pinsky and Byler 2015). Additionally, there is strong support that boom-bust population cycles are exacerbated by commercial fisheries (Essington et al. 2015; Trochta et al. 2020). Forage fishes support some of the world's largest commercial fisheries, representing 30-37% of global catch by weight (Alder et al. 2008; Essington et al. 2015), and total landings are valued at an estimated $5.6 billion (USD) each year (Pikitch et al. 2014).

1.2 Atlantic herring biology

A common species of forage fish is Atlantic herring (*Clupea harengus*, hereafter referred to as herring), which are distributed throughout the high latitude waters of the Atlantic Ocean. Herring become sexually mature at two to four years of age and live up to 15-20 years, reaching sizes up to 40-44 cm (DFO 2015, FRCC 2009). Herring exhibit distinct reproductive strategies with variable timing of spawning (typically as either spring- [before July 1st] or fall-spawners [after July 1st]) and strong site fidelity that allows for stock delineation for fishery management (Geffen 2009; Melvin et al. 2009; Stephenson et al. 2009). Outside of the spawning period, adult herring from different spawning components may aggregate together (Wheeler and Winters 1984), migrating several times a year between open ocean feeding grounds and inshore coastal areas for spawning and overwintering (Lambert 1984; Geffen 2009; Stephenson et al. 2009).

Herring distribution in the Northwest Atlantic ranges from Cape Hatteras at the southern extent to Labrador at the northern extent, with stocks broadly defined by spawning areas and coastal state boundaries (Sinclair et al. 1985; Stephenson et al. 2009). From south to north, major stocks include the Gulf of Maine/Georges Bank, the Maritimes (Bay of Fundy and Scotian Shelf), Gulf of St. Lawrence, and Newfoundland, all of which contain numerous, unique subpopulations with variable spawning strategies (Melvin et al. 2009; Stephenson et al. 2009). All stocks support commercial herring fisheries, the largest of which was the Georges Bank stock which peaked in 1968 with 374,000 tonnes of herring harvested (Melvin and Stephenson 2007), but stock conditions throughout most regions

have generally declined in the past several decades. While total allowable catch for herring has rarely, if ever, been exceeded in the Maritimes and Gulf of St. Lawrence since the late 1980s, recent estimates of spawning stock biomasses were below limit reference points (LRP), the threshold of the critical stock status zone (DFO 2006), for at least one management area within both of these stock complexes (McDermid et al. 2018; Boyce et al. 2019; DFO 2020a, 2020b). Similarly, the spring-spawning population in western Newfoundland is also below its LRP (DFO 2018a), and the recruitment estimates of the Gulf of Maine/Georges Bank stock have remained poor since the mid-2010s (NEFSC 2018). In contrast, herring stocks in eastern Newfoundland, which are distinct from the western Newfoundland stock (Moores and Winters 1984), are considered to be less-exploited than other North Atlantic stocks (Winters and Wheeler 1987), and while most of the stock complexes are considered healthy, they are data-poor (Bourne et al. 2018).

The marine ecosystem in eastern Newfoundland is primarily influenced by the inshore branch of the Labrador Current (LC), which transports cold, fresh meltwater from the Arctic and more saline Atlantic water at depth (Lazier and Wright 1993, Cuny et al. 2001, Sheldon et al. 2015). Climate conditions in the North Atlantic cooled dramatically in the late 1980s, resulting in colder sea surface temperatures, changes in ocean transport, and strengthened northern winds (Parsons and Lear 2001). Due to this strong atmospheric forcing, in conjunction with several decades of increasing fishery pressure (Lilly et al. 2013), biomass estimates of both harvested and non-commercial groundfish species of the Newfoundland shelf ecosystem precipitously declined (Pedersen et al. 2017). By the early

1990s, multiple stocks had collapsed, including Atlantic cod (*Gadus morhua*) which was subject to a fishery moratorium in 1992 (Hutchings and Myers 1994). A concurrent collapse of capelin (*Mallotus villosus*), which was the main prey species of the 'wasp-waist' Newfoundland ecosystem (Carscadden 2002), also occurred in the early 1990s (Rose 2005; Buren et al. 2019). The significant changes in the ecosystem during this time period have been identified as a likely regime shift where the ecosystem transitioned from a groundfish-dominated community to a benthic invertebrate-dominated community, favoring species such as northern shrimp (*Pandalus borealis*) and snow crab (*Chionoecetes opilio*) (Rose et al. 2000; deYoung et al. 2004; Pedersen et al. 2017). Although the anomalously cold climate began to warm by the early 2000s, many stocks have yet to recover to pre-1991 abundance levels, including capelin and Atlantic cod.

In contrast to the infamous collapses of the groundfish and capelin stocks in the early 1990s, the lightly-fished herring stocks remained relatively stable following the regime shift (Bourne et al. 2018). In eastern Newfoundland, herring are managed as distinct stocks across five areas: Bonavista Bay-Trinity Bay, St. Mary's Bay-Placentia Bay, Fortune Bay, White Bay-Notre Dame Bay, and Conception Bay-Southern Shore (Wheeler and Winters 1984; Bourne et al. 2018). As within other stock areas of the North Atlantic, there are both spring- and fall-spawning herring within each stock. Before the early 2000s, the majority of herring in eastern Newfoundland spawned in the spring (Jan. 1 – June 30), while <10% of the population spawned in the fall (after July 1st) (Melvin et al. 2009; Bourne et al. 2018). Since the early 2000s, this trend has reversed, with the majority of spawning now occurring

in the fall (Bourne et al. 2018). The cause of this shift may be related to changing ocean climate and plankton phenology (DFO 2019a).

A change from predominantly spring-spawning to predominantly fall-spawning herring stocks in eastern Newfoundland has the potential to increase the temporal and spatial overlap between adult herring and the early life stages of other fish species in the bays during the fall. Unlike some species of forage fishes which are obligate planktivores, herring are also capable of piscivory (Hardy 1924) which results in a role reversal where the prey (i.e., forage fish) becomes the predator by consuming the upper trophic level predator when it is at its most vulnerable, as either eggs or larvae. Piscivorous forage fish are, therefore, capable of exerting top-down pressure on predator populations (Arrhenius 1997; Cury 2000). The impact of herring predation on early life history stages of fishes could be significant as larvae from 14 different fish families have been observed along the northeastern coast of Newfoundland during the late summer and early fall, including redfish (Sebastidae), shannies (Stichaeidae), flounders (Pleuronectidae), and snailfishes (Liparidae) (Pepin et al. 1995; Stanley et al. 2012). Additionally, Trinity Bay contains multiple beach and demersal (deep-water, < 40 m) sites used by capelin for spawning in mid-to-late July (DFO 2018), and the bay and its eelgrass beds are important nursery areas for Atlantic cod larvae and juveniles throughout the late summer and early fall (Davidson and de Young 1995; Grant and Brown 1998; Stanley et al. 2013). Juvenile and adult herring are known to feed on larval and juvenile fishes, including Atlantic cod and capelin, in the North Atlantic (Cushing 1980; Koster and Mollman 2000; Darbyson et al. 2003; Link et

al. 2009). In the Barents Sea, predation pressure by juvenile herring has been identified as a driver of capelin recruitment (Gjøsæter and Bogstad 1998; Gjøsæter et al. 2016).

Small pelagic predators, such as herring, have been shown to exhibit growth-selective predation, preferentially preying upon slow-growing fish larvae, which are vulnerable to high larval mortality rates (Chambers and Leggett 1987, Takasuka et al. 2007). Given the previous reports of both juvenile and adult herring predation on larval fish and the potential increased temporal overlap of adult herring with the early life stages of other species of fishes in the bays throughout the fall, I hypothesize that the shift in herring spawning phenology has the potential to influence fish recruitment in the region. This thesis aims to describe adult herring diets and feeding strategy with consideration to the potential impacts of herring piscivory in eastern Newfoundland.

1.3 Herring diet

In the Northeast Atlantic, numerous studies have assessed the diet of herring. Herring diet was found to vary both seasonally and spatially, and primarily reflected the seasonality of zooplankton in the region. Adult herring preyed heavily on calanoid copepods, primarily *Calanus finmarchicus*, when copepod abundance was high in the early summer throughout the Norwegian Sea (Dalpadado et al. 2000), North Sea (Segers et al. 2007), and Baltic Sea (Prokopchuk and Sentyabov 2006). In the spring and fall, when copepod abundance was lower, adult herring fed heavily on euphausiids in the Norwegian Sea (Dalpadado et al. 2000) and consumed amphipods, mysids, and polychaetes in the Baltic Sea (Casini et al.

2004). Piscivory was also common. Herring have been found to prey on capelin larvae in the Barents Sea, though primarily by juvenile rather than adult herring (Gjøsæter and Bogstad 1998; Hjermann et al. 2010), on Atlantic cod eggs and larvae in the Baltic Sea (Koster and Mollman 2000; Prokopchuk and Sentyabov 2006), and on both Atlantic cod and plaice (*Pleuronectes platessa*) eggs in the North Sea (Cushing 1980; Segers et al. 2007). One of the few reported year-round studies of herring diet examined age-0 and age-1 herring off the coast of Scotland and found that herring fed on copepods almost continuously throughout the year and other prey items only contributed to their diet on a seasonal basis (De Silva 1973).

In the Northwest Atlantic, there have been comparatively few studies on adult herring trophodynamics. There was an anecdotal observation of larval capelin in herring stomachs in eastern Newfoundland in the 1940s (Templeman 1948). Notably, in the late 1970s, the diet of juvenile and adult herring from the Grand Banks south to Cape Hatteras was described, with herring diet dominated (~97%) by crustaceans, primarily euphausiids, in both the Gulf of Maine and along the Scotian Shelf while herring sampled from Georges Bank primarily consumed chaetognaths (58%; Bowman et al. 2000). In the Gulf of St. Lawrence, adult herring stomach contents have been evaluated sporadically since the late 1980s. Diet composition of adult herring in both the north and south regions of the Gulf was dominated by copepods and other zooplankters, with early life stages of fishes being consumed in the northern Gulf (Savenkoff et al. 2006). More recently, adult herring diets in the southern Gulf of St. Lawrence were found to be primarily comprised of *Calanus* spp.

copepods, both numerically and by wet weight, along with contributions by fishes (predominantly capelin) and euphausiids (Darbyson et al. 2003).

1.4 Approach to diet analyses

Stomach content analysis is the traditional method to evaluate fish diets (Hyslop 1980). The advantages of this approach include ease of sample collection and the fine-scale taxonomic resolution of prey and predator stage (Knickle and Rose 2014). Conversely, the benefits of stomach content analysis can also be considered drawbacks: requiring taxonomic expertise to identify highly-digested prey, the potential to underestimate soft-bodied, quickly digested prey items (e.g., fish larvae), and the temporal window of the diet is limited to the most recently consumed meal. Stable isotopes were first introduced as a complementary means to evaluate food web structures in the 1970s (DeNiro and Epstein 1978; Peterson and Fry 1978; Vander Zanden and Fetzer 2007) and have since been readily adopted as a complementary technique to assess prey contribution to diet (Layman et al. 2012; Perkins et al. 2014). Stable isotopes provide a more comprehensive analysis of diet by reflecting the isotopic signatures of prey items that were integrated into the predator tissue over a period of two to three months (Sherwood et al. 2007). Common stable isotopes in diet analyses are carbon (C^{13}) to differentiate between benthic and pelagic sources of carbon (DeNiro and Epstein 1978), nitrogen (N^{15}) to distinguish trophic levels (Cabana and Rasmussen 1996; Knickle and Rose 2014), and sulfur (S^{32}) which complements carbon to further discriminate between benthic and pelagic sources (Connolly et al. 2004). Drawbacks of stable isotopes include sensitivity to changes in predator growth (Perga and

Gerdeaux 2005), difference in isotopic turnover rates of predator and prey tissues (Vander Zanden et al. 2015), and temporal and spatial environmental variability (Cabana and Rasmussen 1996; Sokolowski et al. 2014). Furthermore, prey taxa that occupy similar trophic levels may be difficult to distinguish by isotopic signatures alone, and require the taxonomic resolution of diets provided by stomach content analyses (Polito et al. 2011). Collectively, stomach content analyses and stable isotopes provide both short-term and long-term insight into predator diets and create a robust approach to diet analyses (Drazen et al. 2008; Polito et al. 2011; Kadye and Booth 2012; Knickle and Rose 2014).

Chapter two: Temporal variation in prey fields and herring diet in Trinity Bay from 2017 to 2019

2.1 Introduction

Atlantic herring (hereafter referred to as herring) is a forage fish that sustains high volume fisheries in the North Atlantic (Alder et al. 2008; Pikitch et al. 2014). It funnels energy between lower trophic levels (i.e., zooplankton) and larger predators, such as piscivorous fishes, seabirds, and marine mammals (Cury 2000; Overholtz and Link 2007). Herring also transport energy from the open ocean to the coast during spawning migrations (Varpe et al. 2005). Similar to other forage fish, boom and bust cycles resulting in an oscillation between periods of extremely high and low abundance characterize herring populations (Toresen and Østvedt 2000; Montero-Serra et al. 2015; Jacobsen and Essington 2018; Trochta et al. 2020). Boom-bust population dynamics have been attributed to changes in environmental drivers that modify prey availability and result in bottom-up control of herring populations (Ottersen and Loeng 2000; Toresen and Østvedt 2000; Payne et al. 2009; Alheit and Peck 2019), although top-down control by commercial fisheries and predation also play a role in forage fish population dynamics (Essington et al. 2015; Jacobsen and Essington 2018).

Traditionally, stomach content analysis has been used to study the diet of herring and document changes in the utilization of food resources (Hyslop 1980). However, this method only provides an instantaneous measure of diet and easily digested, soft-bodied

prey may be underestimated due to rapid gastric evacuation (e.g., 50% gastric evacuation in 1.75 hours for herring in the Gulf of St. Lawrence; Darbyson et al. 2003). In contrast, stable isotope analyses integrate diet over several months, minimizing the bias of rare or infrequently consumed taxa (Sherwood et al. 2007). Combining both traditional diet and stable isotope methods produces a robust analysis that compensates for the weaknesses of each method (Drazen et al. 2008; Polito et al. 2011; Kadye and Booth 2012; Knickle and Rose 2014).

The diet of juvenile and adult Atlantic herring has been investigated using stomach content analyses on both sides of the North Atlantic. Calanoid copepods, specifically *Calanus finmarchicus* and *Calanus hyperboreus* and, to a lesser extent, euphausiids, represent the primary prey items in herring diets (Koster and Mollman 2000; Darbyson et al. 2003; Prokopchuk and Sentyabov 2006; Segers et al. 2007). Secondary prey items vary regionally. Amphipods are commonly detected in diets of Baltic, Norwegian, and North Sea herring (Koster and Mollman 2000; Prokopchuk and Sentyabov 2006; Segers et al. 2007), while chaetognaths and mysids are common in the diet of Gulf of St. Lawrence and New England herring (Bowman et al. 2000; Savenkoff et al. 2006). Juvenile, and, to a lesser extent, adult Atlantic herring also consume fish larvae when they are present (Huse and Toresen 2000; Darbyson et al. 2003; Hallfredsson et al. 2007; Hallfredsson and Pedersen 2009). In the Barents Sea, juvenile herring feed heavily on larval capelin, and juvenile herring abundance has been related to recruitment variability of capelin in the region (Gjøsæter and Bogstad 1998; Hjermann et al. 2010).

In contrast to the rest of the North Atlantic, information on the diet of herring in eastern Newfoundland is scarce. A study from the 1940s revealed predation on capelin larvae in Fortune Bay, located on the southeast coast of Newfoundland (Templeman 1948). However, the diet of herring from the northeast coast of Newfoundland remains unknown. Herring populations in this region have recently exhibited a change in spawning phenology, shifting from a spring-spawning population (estimated >90%) to predominantly fall-spawning in the early 2000s (Bourne et al. 2018). Of the five stocks in eastern Newfoundland, the most pronounced shift occurred in the Bonavista Bay-Trinity Bay stock complex, where fall-spawners now represent 80% of the population based on catch data (Bourne et al. 2018). Herring begin feeding immediately after spawning inshore, which potentially increases the predation pressure on the early life stages of capelin and Atlantic cod (*Gadus morhua*) that are present in the northeastern bays in late summer and fall (Baumann et al. 2003; Stanley et al. 2012, 2013). However, the lack of herring diet data from Newfoundland coastal ecosystems limits our understanding of the trophodynamics in the region.

Here I examine the fall diet of adult herring in relation to available prey fields and the environment in Trinity Bay from 2017-2019 to characterize adult herring prey selectivity and both intra- and interannual variability in diet composition. Specifically, I use ichthyoplankton and oceanographic survey data from late summer and early fall (August and September) to describe plankton communities and water column characteristics. I

then examine herring diet from August to November using a combination of stomach content and stable isotope analyses. Finally, I compare the available prey fields with the consumed prey in herring diets to assess selectivity and variability among months and years. By describing adult herring feeding strategies and identifying key prey items, this study aims to improve our understanding of the ecology of herring.

2.2 Methodology

Study area

Trinity Bay (48.0 °N; 53.5 °W), located on the northeast coast of Newfoundland, is approximately 100 km long by 30 km wide (Yao 1986, Dalley 2002) (Fig. 1). The mouth of the bay is oriented to the northeast and features a large sill at 240 m (Baumann et al. 2003). The maximum depth is 630 m, though the majority of the bay is less than 300 m deep (Parrish 1998; Baumann et al. 2003). The inshore branch of the Labrador Current transports water of Arctic origins (Lazier and Wright 1993) into the bay from the northern side of its mouth, circulates counter-clockwise within the bay, and exits along the southern side of its mouth (Yao 1986, Tittensor et al. Dalley 2002, Baumann et al. 2003). Throughout the summer months, a pycnocline forms at approximately 25 m below the surface (Yao 1986).

The two sites identified for sampling of adult herring, Hickman's Harbour and New Harbour (Fig. 1), were selected based on historical research efforts and harvester availability. Hickman's Harbour is situated in the Northwest Arm of Random Sound along

the western side of Trinity Bay and has a maximum depth of approximately 150 m (Wroblewski et al. 1994). New Harbour is a small cove located in southeastern Trinity Bay and is open directly to the bay with a depth of <100 m (Baumann et al. 2003).

Oceanography and zooplankton

Physical properties and plankton composition were sampled by Fisheries and Oceans Canada (DFO) in mid-August and September from 2017 to 2019, primarily along two transects parallel to the mouth of the bay and approximately three nautical miles apart, for a total of 6-10 stations sampled per survey (Fig. 1). In 2017, a Seabird 12 salinity-temperature-depth (STD) profiler was attached to bongo nets to collect temperature and salinity profiles, and in 2018-2019, a Seabird 19 Plus conductivity-temperature-depth (CTD) was used to profile the water column. Variations in temperature and salinity were minimal within each survey due to the proximity of stations and the bathymetry of the bay (i.e., the sill increases water retention times). Therefore, all CTD casts were pooled along Transect A (the transect with the highest sampling frequency; Fig. 1) to characterize the water column characteristics for a given survey. Casts were averaged by 1-m depth bins to create representative temperature and salinity curves for each month. The CTD malfunctioned at stations 35 and 36 in August 2017 and station 32 in August 2019 so these profiles were omitted from the analysis.

Plankton was collected using methods described in Dalley (2002). Briefly, bongo nets of 61 cm diameter with 333μm mesh nets were deployed in an oblique pattern to 10 m off the

seafloor at each station or to a maximum of 200 m depth. The nets were deployed at a winch speed of 20 m min^{-1} on the descent and 10 m min^{-1} on the ascent, with a vessel speed of 2-2.5 knots. General Oceanic flowmeters were attached to the mouth of each net to determine the volume of water filtered. The contents of one side of the bongo nets were preserved in 5% formalin for larval fish identification (no eggs were enumerated). The contents of the second side were immediately frozen in seawater for zooplankton identification and stable isotope analysis.

Larval fishes from formalin-preserved samples were sorted, enumerated, and identified at the Northwest Fisheries Science Center, St. John's, Canada. Frozen plankton samples were identified at the Université du Québec à Rimouski, Canada. Samples were diluted to known volumes approximately 1000-2000 mL with 10-30 mL subsampled, and zooplankton were enumerated and identified to the lowest taxonomic level possible. Copepods were staged (C1-C6) and sexed (adult stages). Plankton samples designated for stable isotope analysis were identified to the lowest taxonomic level possible. Taxa were either processed individually or grouped based on organism size to produce approximately 1.0 mg dried weight (e.g., Calanoid copepods were grouped while an individual euphausiid was used).

I calculated the density of identified zooplankton taxa and larval fishes (individuals$\cdot m^{-3}$) for all stations to assess the prey fields available to herring in August and September. For general comparisons, the mean and standard error (SE) were calculated across all stations, and the average total zooplankton density was calculated for each survey. To differentiate

between plankton communities at all stations, I conducted a cluster analysis using e-PRIMER 6.0 software (Clarke 1993). Plankton densities were fourth-root transformed to equalize variance among species, and a Bray-Curtis similarity index was calculated. I determined which plankton taxa contributed to differences among cluster groupings using a similarity percentage analysis (SIMPER).

To determine the drivers of variability in plankton density between surveys, temperature, salinity, and month/year were used as variables in a distance-based linear model (DistLM) with forward selection and adjusted R^2 to order the importance of the independent variables. Salinity and temperature profiles were averaged at the surface (0-10 m) and at depth (180-190 m, which is the deepest interval possible across all stations). Temperature and salinity were normalized and Euclidean distances calculated. A permutational multivariate analysis of variance (PERMANOVA) test, informed by the order determined by the DistLM, was used to assess the effect of temperature, salinity, and time on plankton density.

Herring sample processing

To assess the late summer and fall diet of adult herring, I sampled adult herring over ~12 weeks each fall from 2017-2019. Survey design and gear were based on the Canadian Department of Fisheries and Oceans Canada (DFO) herring research gill net surveys conducted since the early 1980s (Bourne et al. 2018). Herring were collected biweekly from August to October in 2017 and once a week from August to November in 2018 and

2019 (Table 1). Gillnets consisted of five multifilament nylon panels, measuring 34.3 m by 200 meshes deep with mesh sizes ranging from 50.8 to 76.2 mm in increments of 6.35 mm. The selected mesh sizes target the complete size range of adult herring, including the minimum size targeted by the commercial fishery (24.76 cm). Harvesters set the gillnets at sunset and pulled the nets approximately one hour after sunrise when herring stomach fullness is at its peak (Darbyson et al. 2003). I collected the first ten fish encountered in good physical condition (i.e., free of major abrasions or entanglements) in each gillnet for a maximum of 50 fish per sampling event. Only fish alive at the time of capture were selected to maximize the probability that the fish had recently fed. Herring were euthanized using a mixture of clove oil and ethanol (~50 mL, 1 part clove oil to 9 parts 99% ethanol added to a seawater bath) and immediately flash frozen on dry ice to halt further digestion and preserve the stomach contents. In 2018-2019, the first five fish from each length bin (5 cm bins, range 20-40 cm) were subsampled for stable isotopes by removing a 1.25 cm^2 muscle plug from below the dorsal fin (Perga and Gerdeaux 2005), and the tissue sample was flash frozen. Clove oil euthanasia does not have an impact on the stable isotope signatures of fish (Hanisch et al. 2010; Demopoulos and Sikkel 2015).

Herring were thawed in the laboratory and measured (Total Length, TL), weighed (total, gutted, and gonad; adjusted to include the removed tissue sample), and sexed. Herring were assessed for maturity stage by DFO technicians based on Parrish and Saville (1965; Appendix A). A single reader from DFO with 20+ years of expertise aged the otoliths of a random subset of 695 herring based on annulus formation. The reader also assigned a

spawning component for each aged fish as either spring (January 1st – June 30th) or fall (July 1st – December 31st) based on fish age, maturity, individual otolith characteristics, and season of capture (see Wheeler et al. 2009 for details). Stomachs were removed with excisions anterior to the cardiac sphincter and posterior to the pyloric sphincter (Cunha et al. 2005) and re-frozen for later processing.

There was no significant difference in lengths of herring sampled from the two sampling sites (Kruskal Wallis, p-value = 0.3052; Appendix B). Since the aim of this study was to describe the diet of adult herring, I pooled all herring across sampling sites and lengths, as all were mature adults, and I investigated trends in the diet at the monthly and yearly scale. A single sample collected in November 2019 was omitted due to small sample size (n=4).

Herring diet analyses: stomach contents

Individual stomachs were thawed, weighed, and the stomach contents were removed to obtain the wet bolus weight. A Wild M3Z microscope (6.5-40.0X) was used to identify and measure prey. All prey items were enumerated, identified to the lowest taxonomic level possible given the degree of digestion, and collectively weighed by taxa. While some prey were identified to species or genus, prey item categories (hereafter, prey items) were limited by the coarsest level of taxonomic resolution and pooled as such (e.g., some amphipods identified to species, but others only as Amphipoda so all were grouped as Amphipoda). When feasible, individual prey lengths were also measured (mm). All fish larvae in the stomachs were identified to the lowest taxonomic level possible. Any samples

with perforations of the stomach cavity as well as any stomachs that were not fully intact were omitted from the analysis. Any stomach material that was unidentifiable due to digestion was also omitted.

I assessed herring diets in each month of sampling using four metrics: 1) gravimetric weight, 2) mean partial and total fullness index (PFI and TFI, respectively), 3) frequency of occurrence, and 4) prey-specific abundance. The average gravimetric weight proportion provided an estimate of prey contribution to diet by weight and was calculated by:

$$\% \, G_i = \sum_{k=1}^{n} \frac{S_{ik}}{S_k}$$

where S_{ik} is the weight (g) of prey item *i* in the stomach of herring *k*, S_k is the total weight (g) of all prey items in the stomach of herring *k*, and *n* is the number of stomachs (Hyslop 1980). Prey items that contributed < 5% to gravimetric weight in a given month were pooled as 'Other'.

Mean PFI provided a measure of stomach fullness for each prey item within a sample, accounting for length differences of herring and was calculated by:

$$PFI_i = \frac{1}{n} \sum_{k=1}^{n} \frac{S_{ik}}{(L_k)^3} \times 10^4$$

where S_{ik} is the weight (g) of prey item *i* in the stomach of herring *k*, *n* is the number of stomachs, and L_k is the total length (cm) of herring *k* (Lilly and Fleming 1981; Dalpadado and Bogstad 2004).

The mean TFI provided a measure of total stomach fullness across all prey items, accounting for fish length and was calculated by:

$$TFI = \frac{1}{n}\sum_{k=1}^{n}\frac{S_k}{(L_k)^3} \times 10^4$$

where S_k is the total weight (g) of all prey items in the stomach of herring *k*, and L_k is the total length (cm) of herring *k* (Lilly and Fleming 1981; Dalpadado and Bogstad 2004).

Frequency of occurrence provided an estimate of the presence of prey items across all herring diets and was calculated by:

$$\%\, F_i = \frac{n_i}{n}$$

where n_i is the number of stomachs containing prey item *i*, and *n* is the total number of stomachs. Only prey categories with >5% frequency for a given month were included.

Prey-specific abundance was calculated using a graphical analysis (Costello 1990, Amundsen et al. 1996) to examine feeding strategy, prey selectivity, and resource use at the individual and population level. The graphical analysis of feeding strategy plots the frequency of occurrence by a prey specific abundance, calculated by:

$$P_i = \left(\frac{\sum S_i}{\sum S_{ij}}\right) X\ 100$$

where S_i is the weight (g) of prey item *i* in herring stomachs, and S_{ij} is the total weight (g) of all prey items in the stomach of herring which fed on prey *i*. The position of prey items

on the plot from the lower-left to the upper-right corners reflects the relative importance of the prey item in herring diet (increasing from left to right) while the position of prey items along the y-axis indicates either a generalized (low values) or a specialized feeding strategy (high values) (Amundsen et al. 1996). The position of prey items on the plot from the upper-left to the lower-right corners indicates niche width contribution, differentiating between high between-phenotypes (individuals focusing on different resources) and high within-phenotypes (population-level predation upon a range of common prey items).

Finally, to evaluate piscivory in the diet, I first pooled all fish data (i.e., egg, eggs and gravel, larvae, juvenile/age-1 fishes as well as fish remnants such as skeletons, otoliths, tissue) into a collective 'teleost' category for each diet metric. I also evaluated these early life stages separately using both frequency of occurrence and gravimetric weight analyses and included all values (no 5% cutoff) to further examine potential patterns of piscivory.

Herring diet analyses: stable isotopes

Frozen herring tissue and zooplankton samples for stable isotopes analysis were freeze-dried for approximately 24-72 hours, dependent on sample batch size, and pulverized to a fine powder using a sterilized mortar and pestle. Zooplankton samples were processed as whole organisms, consistent with previous studies (Logan et al. 2008; Pomerleau et al. 2014). Samples were analyzed at the Cornell Stable Isotope Laboratory. Stable isotope ratios of C^{13} and N^{15}, as well as elemental C:N, were measured using a Thermo Delta V Advantage mass spectrometer, plumbed to a Carlo Erba NC2500 Elemental Analyzer via

a ConFlo III interface. Samples were matched against in-house standards calibrated against international standards. Error, as assessed by sample replicate analysis, was 0.18‰ for $\delta^{15}N$ and 0.17‰ for $\delta^{13}C$. Delta values for C^{13}/C^{12} and N^{15}/N^{14} were calculated using

$$\delta_{sample-standard}(‰) = \left[\frac{R_{sample} - R_{standard}}{R_{standard}}\right] * 10^3$$

with R_{sample} representing the ratio of heavy isotope to lighter isotope in the sample, $R_{standard}$ is the ratio of heavy to light isotope in the reference sample calibrated against international standards, and $S_{sample-standard}$, either $\delta^{13}C$ or $\delta^{15}N$, is expressed as parts per-mille (‰).

It is essential to correct for lipid variability as many organisms accrue large lipid stores in summer months, particularly in high latitude regions (Hagen and Auel 1999). Lipid content is negatively correlated with $\delta^{13}C$ values and is known to vary between species as well as differ temporally among individuals and different types of tissue (Parker 1964, Focken and Becker 1998). This bias can produce artificial differences in carbon isotope ratios and must be accounted for before interpretation. Although lipid extraction before stable isotope analysis is ideal (Mintenbeck et al. 2008), treatment of samples may result in depleted $\delta^{15}N$ values (Logan et al. 2008; Pomerleau et al. 2014). Species' tissue-specific corrections were not available for all taxa so the following standard lipid correction for aquatic animals (Post et al. 2007) was applied *a posteriori*:

$$\delta^{13}C = 0.99 * C{:}N_{ratio} - 3.32$$

Inorganic carbon is common in calcifying marine organisms and has also been identified as a potential source of bias of $\delta^{13}C$ values (Wada et al. 1987). A carbonate correction (Pomerleau et al. 2014) was thus applied to the shelled pteropods, *Limacina* spp.:

$$\delta^{13}C_{acid} = 0.994 * \delta^{13}C_{bulk} - 1.096$$

Although crustaceans also have exoskeletons, they are primarily comprised of chitin rather than calcium carbonate, and there is no significant difference in $\delta^{13}C$ between acidified and untreated samples (Pomerleau et al. 2014).

I described herring stable isotopes by calculating the mean, SE, and range of herring signatures for each month and used Spearman rank correlations to determine if changes in lipid-corrected $\delta^{13}C$ and $\delta^{15}N$ were significant between months and years. Both isotopic signatures were also evaluated with consideration to trophic discrimination factors, or fractionation (e.g., $\Delta\delta^{13}C$ or $\Delta\delta^{15}N$ from prey to predators in which isotopes in predators become slightly enriched through assimilation; Post 2002; Olive et al. 2003). Carbon is thought to vary minimally between trophic levels in the marine environment with 0‰ as the generally applied value (DeNiro and Epstein 1978; Barnes et al. 2007), while 3.4‰ is the estimated fractionation value for nitrogen (Minagawa and Wada 1984; Post 2002). It was clear from the stomach content analysis that not all prey items were represented in the stable isotope samples, so I did not attempt to apply mixing models or calculate niche breadth (Matthews and Mazumder 2005; Phillips et al. 2014), both of which require the full array of prey items.

All statistics were performed using base R v. 1.0.143 (R Core Teams 2016). The data were non-normal hence nonparametric tests were used for the diet analyses.

2.3 Results

Oceanography and plankton prey fields

The oceanography of Trinity Bay in August was similar across all years with warm, fresher water at the surface (10.5-16.6°C and salinity 29.8–31.9) with a thermocline between 10-20 m (Fig. 2). The surface waters in August 2017 were warmer (16.6°C vs. 10.5-11.4°C) and fresher (29.8 vs. 31.6-31.9) than either 2018 or 2019. The oceanography of Trinity Bay in September varied interannually, particularly in the depth of the mixed layer and thermocline. Surface temperatures in September were warm (10.6-12.5°C) and less saline (30.3-30.8) but with a deeper, more variable thermocline between 25-70 m (Fig. 2). The shallowest thermocline in September was observed in 2017 at only ~30 m depth. In September 2019, cooler surface temperatures (10.5 vs. 11-12°C) and a deep thermocline (70 m depth) suggests increased mixing in the upper levels of the water column relative to other months and years.

Prey fields

Secondary production was highest in 2018, followed by 2019 and 2017, with September generally more productive than August although these trends were statistically insignificant (Kruskal Wallis tests: month effect: $p=0.513$ and year effect: $p= 0.651$; Fig. 3a-b). A total of 57 different zooplankton and larval fishes were identified (ranging from

species to phylum) in the ichthyoplankton samples, with 26 zooplankton and larval fishes identified to species, and 11 identified to genus (Tables 1 and 2; Appendix C). Only 12 zooplankton and ichthyoplankton taxa were present throughout all six surveys: seven genera of copepods (*C. finmarchicus, C. hyperboreus, Centropages hamatus, Paracalanus* spp., *Metridia longa, Temora longicornis, Oithona similis,*), ostracods, chaetognaths, euphausiid larvae, gastropods, and capelin.

Copepods were the most abundant taxa by nearly an order of magnitude throughout all surveys with seasonal patterns detected in 2018 and 2019 (Fig. 3a). *Pseudocalanus* spp. comprised 58-62% of the copepod composition in August 2018 and 2019, while *Temora longicornis* comprised 44.3-61.6% of the copepod composition in September 2018 and 2019 (Fig 3a and Table 2). There was no trend in *Calanus* spp. densities, with *Calanus* spp. comprising between 15-37% of the copepod composition for a given month (Fig. 3a). The dominant copepod developmental stage varied by genera (Appendix D). *Calanus* spp. was the only genus to show development between months, with most individuals maturing from either CII and CIII in August to CIV and CV in September (Appendix D). Both *Pseudocalanus* and *Temora* had one dominant developmental stage (CV and CVI, respectively) in both months (Appendix D).

There was seasonal variability in densities of other key plankton taxa, including cladocerans, gastropods, chaetognaths, and fish larvae (Fig. 3b and Table 2). Cladocerans were dominant in August 2017 and 2018, while gastropods were dominant in September

2018 and 2019 (Fig. 3b). Chaetognaths were present at higher densities in September than August (means of 1.92-4.66 m^{-3} vs. 0.38-2.38 m^{-3}) with the highest densities observed in 2019. Fish larvae were observed at low densities relative to other plankton (<1.00 fish m^{-3}) but were consistently present throughout the study (Table 3 and Fig. 3b). Capelin larvae were consistently the dominant species of fish observed. No trends in larval abundance were found, though the highest abundance and diversity of fishes was observed in August 2017 and September 2019.

The cluster analysis revealed six, statistically distinct communities of zooplankton across all years with communities more similar from August 2017 to August 2018 and more dissimilar from September 2018 to September 2019 (Fig. 4 and Appendix E). Copepods (namely *Calanus*, *Pseudocalanus*, and *Temora*) consistently dominated the zooplankton communities, so the similarity between groups was set at a high cutoff (72%; Appendix E) and small differences in the contribution of less common taxa drove the dissimilarity (Table 4). Two groups, A and B, occurred exclusively in 2017 and August 2018 and were characterized by the high contributions of *Evadne* spp., *Acartia* spp., and euphausiids (Table 4 and Fig. 4). Group C included only three stations between both September 2017 and August 2018 and was distinguished by high contributions of *Metridia* spp. and ostracods (Table 4). Intra- and inter-annual variability increased after August 2018, with all stations from September 2018, August 2019, and September 2019 forming distinct groups (Fig. 4). High contributions of copepods (namely *Calanus*, *Pseudocalanus*, and *Temora* as well as *Metridia* and *Oithona*) helped distinguish communities in 2019 (groups

E and F) relative to other years which had increased contributions of other non-copepod taxa (Table 4).

Environmental factors were a strong driver of plankton variability (Table 5). The DistLM analysis found all environmental variables to be significant (p= 0.001) in defining plankton communities (Table 5). The ordered environmental variables were then incorporated into the PERMANOVA with a joint year-month factor, which explained over 85% of the observed variability (Table 5). Collectively, environmental variables explained more than 73% of the variability, with average bottom salinity being the primary driver of plankton communities. The temporal factor, accounting for both month and year, explained 12.8% of the variation.

Herring diet analysis

A total of 1,260 herring stomachs were analyzed in this study (541 in 2017, 451 in 2018, and 268 in 2019) (Table 1). Herring ranged in sizes from 25.1 to 40.0 cm TL, and the average length in each month and year was similar at 32 cm TL (Table 1). Ages ranged from 3 to 11+ years (maximum age counted; Table 1) and there was a significant difference in the age of herring between spawning components (Kruskal-Wallis, p-value=$2.0e^{-17}$) with fall-spawners generally two to three years older than spring-spawners in a given month (Appendix G). The average maturity stage across all months was 4, indicating that most individuals were mature but pre-spawning (Table 1). A total of 152 stomachs were empty (12.0% of all processed herring; Table 1). Feeding incidence, the number of stomachs

containing prey relative to the total number of stomachs examined, ranged from 0.65 to 0.95 and peaked in September of all years (Table 1). The TFI values ranged from 0.04-0.56 across all months, with fullness generally increasing from August to October in all years (Table 1). Stomach fullness (TFI) typically tripled from September to October in all years though stomachs in 2019 had the lowest fullness in all months of the time series. There were no significant differences in diet between spawning components in TFI values (Kruskal-Wallis, p-value=0.456; Appendix H).

Zooplankton prey in herring diet

The two prey items that contributed most to herring diets by weight were amphipods and copepods and they had an inverse relationship (Fig. 5a-b). Amphipods consistently comprised a large proportion of the diet by weight until September 2018 and thereafter copepods comprised a larger proportion of the diet (Fig. 5b). Amphipods and copepods both had high frequencies of occurrence in herring diet, but the proportion of the population feeding on these prey items differed (Fig. 6). Amphipod consumption ranged between 8-64% each month, while copepods were consistently consumed by >60% of the herring population, except for anomalously low frequency of occurrence in October 2017 which coincided with peak amphipod consumption (Fig. 6). The PFI analysis revealed similar trends, showing that amphipods and copepods were important prey items by weight but indicates that copepods overall contributed less to diets once herring weight (and therefore consumption capacity) was accounted for (Fig. 5a-b).

In addition to amphipods and copepods, two additional taxa were identified as key contributors to herring diet in the PFI, gravimetric weight, and frequency of occurrence analyses: euphausiids and decapods (primarily crab zoea and megalopa). Euphausiids contributed to the diet by weight primarily in August 2017, September 2017, and August 2018 (Fig. 5a-b) and were regularly consumed by 19.1-27.6% of herring (Fig. 6). Similarly, decapods only contributed substantially by weight in September and October 2017 (Fig. 5a-b) and were consumed most frequently in 2017 (frequency of occurrence: 22.9-45.1%; Fig. 6). The remaining 16 prey items identified in the diet (e.g., polychaetes, larvaceans, pteropods, and organic material) occurred infrequently and only sporadically contributed to the diet by weight (Figs. 5a-b and 6). Although spring-spawners had more diversity of prey items in the diet, these items contributed only minimally to the diet by weight, and the main prey items were consumed by both spawning components in nearly all months (Appendix H).

Herring piscivory

Herring fed on teleosts (pooled early life stages of fishes) in all months of the study (Fig. 7), though teleosts only substantially contributed to diet by weight in 2017 (Fig. 5a-b). Evidence of fish in the stomachs ranged from single, hard structures (bones, fin rays, and otoliths) to intact spines and digestive tracts to reasonably well-preserved whole specimens. Varying degrees of digestion made it difficult to identify most fish larvae in the diets. Capelin represented 57.9% of the fish that were identified. The forage species Arctic cod (*Boreogadus saida,* 21.1%), sand lance (*Ammodytes* spp., 15.8%), and daubed shanny

(*Leptoclinus maculatus,* 5.2%), represented most other fish species in the herring diets (Appendix C and Table 6). Although otoliths appeared to be either capelin or gadids, they could not be reliably paired for counts or identified with certainty due to indeterminate exposure to gastric acid, which can rapidly erode fine structural details in a matter of hours (Jobling and Breiby 1986).

Individual herring often consumed several different life stages of fishes and, when present in the stomach contents, early life stages of fishes were often highly abundant. Maximum numbers in a single stomach included >300 fish eggs in one stomach and 32 fish larvae in another. The largest measurable fish prey was a 7.5 cm capelin (likely either a late-juvenile or age-1 fish). Across all years, fish eggs (present in 131 herring stomachs) were consumed more frequently than larvae (present in 60 herring stomachs) in August and September, and larvae were consumed more regularly in October (Fig. 7a). Predation on fish eggs in August 2018 was unusually low (4.6%) relative to August 2017 and 2019 (23.7 and 29.6%, respectively; Fig. 7a). Fish contribution to herring diet by weight (gravimetric and PFI) did not reflect the trends observed in frequency of occurrence (Figs. 5a-b and 6). This was particularly evident in August and September 2019 when frequency of occurrence was comparable or greater than 2017 but fish contributed little to the diet by weight (Fig. 7). The prey item 'Eggs and gravel' accounted for nearly 10% of the diet by weight in the gravimetric weight analysis in August 2017 (Fig. 5a). Although the frequency of occurrence of early life stages of fishes was generally <1%, the proportion of eggs and gravel by weight in the diet was 7.89% in August 2017 (Fig. 7a-b).

Prey selectivity

Across all sampling periods, individual herring ate a variety of prey items that contributed little to the overall diet (Fig. 8). Herring used a generalized feeding strategy when feeding on cladocerans, though they contributed little to the diet, and on copepods in 2017-18. After August 2018, herring switched to a specialized feeding strategy to consume copepods (Fig. 8). Specialized feeding occurred in all months by at least some individuals of the population (high between-phenotype contribution), which usually concentrated on one to four prey items. Although the preferred prey varied among months, amphipods were the most common prey item herring consumed using a specialized feeding strategy (Fig. 8). Other prey items herring consumed using a specialized feeding strategy included teleosts (all early life stages combined) in 2017, euphausiids in 2017 and August 2018, and decapods in August and September 2017. In the latter half of the study (September-November 2018 and September-October 2019), herring exhibited specialized feeding at the population level (high within-phenotype contribution) for copepods, though individual herring reflected greater variability in prey preference in 2018-2019 relative to 2017 and August 2018 (Fig. 8).

Stable isotope analysis

I analyzed $\delta^{15}N$ and $\delta^{13}C$ stable isotopes of a total of 244 herring and 99 samples of potential prey items collected between August and September 2018 and 2019 (Table 7). Herring isotope signatures remained relatively stable over the survey period in both years

(Fig. 9). The mean $\delta^{15}N$ ranged from 12.28 to 12.71‰ while the range of the mean $\delta^{13}C$ was slightly broader, from -20.22 to -20.87‰ (Table 6 and Fig. 9). Although weak, there was a statistically significant, negative correlation between $\delta^{13}\mathrm{C}$ and month (Spearman rank correlation, ρ = -0.15, p-value = 0.02), as well as $\delta^{13}\mathrm{C}$ and year (ρ = -0.37, p-value = $3.00e^{-11}$), indicating a shift towards a more pelagic source of carbon (more negative $\delta^{13}\mathrm{C}$) within a season and across years (Fig. 9). There was no significant correlation between N^{15} ratios and month (ρ = 0.036, p-value = 0.6), but there was a positive correlation with year (ρ = -0.22, p-value = $6.00e^{-4}$; Fig. 9). Although both isotopic signatures varied between years, only the C^{13} ratios varied significantly intra-annually, which may reflect the migration of herring from coastal areas to the bay in the fall. There was no effect of spawning component on $\delta^{15}N$ nor $\delta^{13}C$ (Kruskal-Wallis, p-value = 0.700 and 0.300; respectively).

The carbon and nitrogen signatures of prey items varied both among individuals, as reflected in larger standard error values, and temporally, shown by fluctuations of the mean over time (Fig. 10). The mean $\delta^{13}\mathrm{C}$ ranged between -18.21 to -23.82‰ for most prey items, except for shelled pteropods, which ranged from -11.98 to -13.93‰ (Table 7 and Fig. 10). As benthic sources of carbon are more enriched in C^{13} than pelagic sources, this suggests that *Limacina* may occupy a more benthic niche than other prey items. Although there was more variability in C^{13} depleted prey items among surveys, euphausiids, chaetognaths, and capelin were characterized by low C^{13} ratios (Fig. 10), which indicates pelagic feeding.

The mean δ^{15}N was broader than that of carbon ratios (6.8 to 13.32‰) and generally had a more extensive range within prey items (Appendix F). Both genera of pteropods, *Limacina* and *Clione*, had the most depleted N^{15} ratios, suggesting a lower trophic position relative to other prey items. Fish eggs had the most enriched N^{15} ratios in August of both years at 13.32 ± 1.84‰ and 12.94 ± 1.62‰ (2018 and 2019, respectively), reflecting the maternal isotopic signatures. Ostracods had the most enriched N^{15} ratios in September 2018 (10.74‰) and chaetognaths in September 2019 (11.36 ± 0.62‰). Other prey items with high $\delta^{15}N$ values included predators such as capelin larvae as well as omnivorous euphausiids, particularly in August of 2019 (Fig. 10; Appendix F). In both years of sampling, there was high variability in N^{15} ratios among fish eggs, euphausiids, and decapods in August. Although sample sizes of prey items were small in both years (n = <5), there was much less variability in the N^{15} ratios in September for the same prey species (when present), which may suggest either a change in diet or change in the nitrogen source of primary producers between the two months.

2.4 Discussion

Importance of the prey field to herring diet

Herring diet closely reflected changes in zooplankton community composition in Trinity Bay. The main prey of herring in late summer and fall in Trinity Bay were amphipods (primarily *Themisto* spp.) and calanoid copepods (primarily *Calanus* and *Temora* spp.), consistent with previous studies throughout the North Atlantic (Darbyson et al. 2003;

Casini et al. 2004; Dommasnes et al. 2004). While herring primarily consumed crustaceans, 18 different prey items were observed in herring stomachs. The wide array of prey items in the diet was reflected in the selectivity analysis which showed that herring fed using both a generalized, or opportunistic, feeding strategy, and a specialized, or selective, feeding strategy. When herring foraged opportunistically, they generally fed on a variety of prey items that contributed little to diet by weight, and when herring fed selectively, they consumed specific prey items during periods of high prey densities in the environment (e.g., larval fish, decapods, and euphausiids before September 2018 and copepods during/after September 2018). Furthermore, there was less variability in herring diet in 2017 and August 2018 when zooplankton communities were more stable, relative to the latter half of the study. The strong similiarities between plankton prey fields and herring diet reinforces previous observations that herring respond to changes in the abundance and composition of lower trophic levels (Flinkman et al. 1998; Casini et al. 2004; Prokopchuk and Sentyabov 2006; Segers et al. 2007).

Differences in the environmental conditions between months explained 73% of the variation in zooplankton communities, primarily driven by changes in bottom water salinity. September 2018 marked a shift from relatively warm (12 – 17°C), consistent oceanographic conditions characterized by stable zooplankton community composition to cooler (10.5- 12°C), more saline oceanographic conditions characterized by temporally unique zooplankton communities. The variability in salinity and temperature conditions is explained, in part, by the increased strength of the Labrador Current (LC) and a more

positive North Atlantic Oscillation Index (NOAI) in 2018 relative to 2017 (DFO 2018b, 2019b). The stronger advection of the LC transported a greater abundance of coastal zooplankton species and Atlantic water below the thermocline, from the shelf into the bay. These waters were mixed by upwelling along the western shore of Trinity Bay (Yao 1986; Stanley et al. 2012, 2013) and, driven by stronger winds associated with a positive NAOI (DFO 2018b, 2019b), resulted in cooler, more saline waters in the upper portion of the water column. Additionally, post-tropical cyclone Dorian passed near Newfoundland in early September 2019, which brought hurricane-force gusts to much of Atlantic Canada (Avila et al. 2020) and likely caused the deeper mixed layer (>50 m) observed in the oceanographic data later that month. My results suggest that changes in the oceanographic conditions modify the zooplankton communities of Trinity Bay. Shifts in the distribution, phenology, and community composition of zooplankton are often attributed to changes in climate (Sanvicente-Añorve et al. 2000; Richardson 2008; Mbaye et al. 2020). Therefore, climate may have cascading impacts on forage fish like herring (Arrhenius 1996; Huse and Toresen 2000; Mollmann et al. 2004; Frederiksen et al. 2006), including in eastern Newfoundland.

Since the mid-2010s, zooplankton communities along the Newfoundland shelf have changed with an overall decrease in biomass but an increase in abundance (DFO 2018b, 2019b). The loss of zooplankton biomass is primarily attributed to diminished numbers of the large-bodied copepod, *Calanus* spp. (DFO 2018b, 2019b). In contrast, total zooplankton abundance has increased due to the higher numbers of smaller-bodied

copepods, such as *Temora* (Pepin et al. 2017), and copepod species associated with warmer waters, including *Pseudocalanus*, *Acartia*, and *Oithona* spp. (Plourde et al. 2002; Brosset et al. 2019, DFO 2019b). The increased abundance of copepods in our samples likely explains the high frequency of occurrence and large contribution of copepods to herring diet by weight observed in the latter half of the study as copepods were a readily available food source. This may partially explain the switch in selective foraging of herring for fish eggs and larvae in 2017 to copepods in late 2018 and 2019 when copepod density increased. The decline of large-bodied copepods in high latitude systems have been reported throughout the North Atlantic and Pacific, and these declines have been attributed to higher temperatures and reduced sea ice (Pitois and Fox 2006; Coyle and Gibson 2017). Given the importance of large copepods to herring diet both in this study and throughout the North Atlantic (Darbyson et al. 2003; Dommasnes et al. 2004; Prokopchuk and Sentyabov 2006; Raab et al. 2012), a shift in dominance from *Calanus* spp. to smaller, less-nutritious copepods could trigger bottom-up effects by impacting the energy budget of herring (Flinkman et al. 1998; Cury 2000; van Deurs et al. 2015).

In Trinity Bay, herring rely on both generalist and specialist feeding strategies. As visual predators, herring are limited to filter-feeding at night but can particle feed during the day, which allows them to select for larger, more mobile prey (Batty et al. 1990; Gibson and Ezzi 1992; Darbyson et al. 2003). Selective feeding is known to be influenced by a suite of factors, including the behavioral and physical characteristics of both predator and prey, as well as the physical environment (Kitchell and Kitchell 1980; Dill 1983; Ranåker et al.

2014; Ljungström et al. 2020). Additionally, shifts in the composition of the prey field are known to affect predation pressure on the early life stages of fishes (Segers et al. 2007). Specifically, it was suggested that capelin larvae might experience a release from herring predation pressure when there were high densities of copepods (Hallfredsson and Pedersen 2009). It is possible that filter-feeding may also have increased in 2019, as filter-feeding is more efficient than particulate feeding at high prey densities, allowing herring to alternate between feeding modes to maximize energy intake while minimizing energy expenditure (Pepin et al. 1988; Gibson and Ezzi 1992). This is consistent with previous theories that plasticity in planktivore diets is an adaptive response to seasonal, highly variable prey fields (Eggers 1978). My results support previous findings suggesting that herring have a broad niche width and are capable of adapting their feeding strategy to best exploit the prey fields they encounter (Gibson and Ezzi 1992).

I found evidence of a piscivorous feeding strategy by herring both in the short-term (stomach content analysis) and mid-term (stable isotope analysis), supporting the idea that ichthyoplankton constitutes a key prey item throughout the summer. This is best exemplified by the range of δ^{15}N ratios of prey items, which is larger than the broadly-applied δ^{15}N fractionation value of 3.4‰ (Post 2002). This suggests that herring are not at isotopic equilibrium with the prey items represented in this study even after accounting for fractionation (Olive et al. 2003), and, therefore, herring are likely feeding on prey items at a higher $\delta^{15}N$ that were not captured in the plankton sampling (e.g., larger fishes, such as age-1 capelin observed in one stomach).

Piscivory in herring

Fish eggs and larvae were consistently present in herring stomachs throughout all months of the study and, at peak consumption, represented nearly a third of herring diet by weight. Herring selected for the early life history stages of fishes when larval abundance was at its peak in 2017, similar to previous reports in the North Sea (Segers et al. 2007) and Baltic Sea (Koster and Mollman 2000), as well as juvenile herring diets in the Barents Sea (Gjøsæter and Bogstad 1998). Capelin larvae were the most prevalent fish species in herring diet, although other forage fish species such as sand lance and Arctic cod were also preyed upon. Although otolith identifications could not be validated, it is also likely that Atlantic cod were consumed as reported in other regions (Koster and Mollman 2000).

While fish eggs were not identified to species in this study, the occurrence of eggs attached to gravel in the diet suggests that herring may prey upon capelin eggs at demersal spawning sites. Capelin preferentially spawn along beaches but move to demersal sites when temperatures exceed 12°C (Nakashima and Wheeler 2002). Presently, capelin spawn approximately three weeks later compared to 1980s (Murphy et al. 2018), which increases the likelihood that capelin experience warmer temperatures at beaches. This may result in a greater proportion of capelin eggs being deposited at demersal sites, where they develop more slowly (Nakashima and Wheeler 2002), and thus are more vulnerable to predation by other fish species as herring. Heavy predation on capelin eggs has already been documented in winter flounder (*Pseudopleuronectes americanus*) and it was theorized that

top-down control by predation might influence capelin recruitment (Frank and Leggett 1984). Although herring also produce adhesive, benthic eggs and cannibalism of eggs has been reported (Skaret et al. 2002), herring deposit eggs on kelp and kelp was not observed in herring diet in this study. Based on my observation of eggs and gravel in herring diets and known predation on capelin eggs by other species, herring may also be capable of exerting predation pressure on capelin eggs as well as capelin larvae. Further research is required to evaluate the potential predation pressure exerted by herring on early life stages of fishes.

Diet of adult herring in NL compared to other regions

The findings from this study are consistent with previous observations of herring diet throughout the North Atlantic, specifically the influence of zooplankton seasonality on juvenile and adult herring feeding strategies and diet composition (Casini et al. 2004; Prokopchuk and Sentyabov 2006; Segers et al. 2007). In all months studied, herring consistently consumed calanoid copepods, previously identified as a key prey item for herring (e.g., Darbyson et al., 2003; Dommasnes et al., 2004; Raab et al., 2012), but the greatest contributions of copepods to herring diet in Trinity Bay were observed when there was peak copepod abundance in the environment (e.g., Dalpadado et al. 2000). This was also true for fish eggs and larvae, as adult herring selected for the early life history stage of fishes when larval abundance was at its peak in 2017, and supports previous reports of piscivory in both juvenile (Gjøsæter and Bogstad 1998) and adult herring diets (Koster and Mollman 2000; Darbyson et al. 2003; Segers et al. 2007). This indicates that herring,

regardless of life stage, may exert top-down predation pressure on the early life stages of fishes whenever there is an overlap in distribution. Herring in Trinity Bay also selected for other seasonally important prey items identified in the literature, including amphipods and euphausiids (Casini et al. 2004) as well as decapods (De Silva 1973).

Conclusion

This study provides rare baseline data on late summer and fall adult herring diets in eastern Newfoundland, laying the foundation for future comparative studies across different seasons and spatial scales. Influenced by Arctic currents, the waters surrounding Newfoundland represent a low-latitude boreal ecosystem that will likely experience significant changes due to climate warming in the decades to come. Forage fish such as herring represent a critical trophic link in marine food webs and are particularly vulnerable to climate change through bottom-up processes related to the phenology, abundance, and composition of their zooplankton prey (Raab et al. 2012; Hill et al. 2015). This study demonstrates that, in eastern Newfoundland, adult herring also has the potential to be drivers of food web changes through top-down processes of predation on zooplankton and larval fishes. As herring are opportunistic feeders with a broad niche and plasticity in their diet, herring may be more resilient than other species to environmental changes. Further research is, however, essential to understand how herring and their ecosystems will respond to climate change and to support the sustainable management of forage fishes.

2.5 Tables

Table 1. Summary of all herring sampled by month. Of the 1,260 total fish suitable for stomach content analysis, 1,114 contained prey items and were included in the diet analyses. Of the 260 herring muscle samples collected for stable isotope, 244 had complete data available for this study. Spawning component and age data were available for a subset of herring collected (n=695). SCA: stomach content analysis, SIA: stable isotope analysis, SR: spawner ratio (fall:spring), FI: feeding incidence (stomach containing prey:total stomachs), TFI: total fullness index. Average total length, age, and maturity stage (mean ± SE) for each month of sampling are presented.

	SCA	SIA	SR	FI	TFI	Total length (cm)	Age (years)	Maturity stage
Aug-17	290	-	0.99	0.90	0.12	32.75 ± 0.21	7.94 ± 0.17	3.91 ± 0.05
Sep-17	204	-	1.27	0.91	0.16	31.26 ± 0.24	6.56 ± 0.18	3.99 ± 0.08
Oct-17	47	-	1.35	0.65	0.49	31.48 ± 0.53	6.93 ± 0.42	3.59 ± 0.18
Aug-18	92	15	1.19	0.70	0.06	32.58 ± 0.33	7.33 ± 0.71	4.01 ± 0.09
Sep-18	119	50	0.75	0.93	0.13	31.30 ± 0.25	6.46 ± 0.33	4.24 ± 0.08
Oct-18	194	70	0.80	0.86	0.56	31.15 ± 0.17	6.51 ± 0.34	3.57 ± 0.07
Nov-18	46	14	1.42	0.86	0.04	31.84 ± 0.37	7.35 ± 0.78	3.34 ± 0.11
Aug-19	33	20	0.94	0.81	0.05	31.14 ± 0.35	6.77 ± 0.45	4.66 ± 0.29
Sep-19	117	45	1.17	0.95	0.04	31.85 ± 0.22	7.13 ± 0.38	4.64 ± 0.13
Oct-19	118	46	1.46	0.92	0.12	31.81 ± 0.20	6.93 ± 0.33	4.18 ± 0.12
Total	1292	260						

Table 2. Average station density (individuals m-3) of all zooplankton sampled with the bongo nets, identified to the lowest possible taxonomic level (mean ± SE). Taxa without a standard error reflect single occurrences. Bold text indicates coarser taxonomic level (mean ± SE). Taxa without a standard error reflect single occurrences.

		2017		2018		2019	
Taxa	Stage	Aug	Sept	Aug	Sept	Aug	Sept
Cnidaria		0.54 ± 0.14	0.92 ± 0.32	1.13 ± 0.50	1.95 ± 0.67		
Polychaete	larvae	0.56 ± 0.17	0.36 ± 0.06	0.69 ± 0.22	0.37		
Cladocera							
Evadne spp.		16.89 ± 8.98	3.20 ± 0.76	34.92 ± 18.87	4.10 ± 1.34	2.43 ± 0.89	
Podon spp.				0.47	0.63 ± 0.06		1.05 ± 0.20
Ostracoda		0.32 ± 0.11	0.65 ± 0.47	0.75 ± 0.06	1.84 ± 1.10	1.16 ± 0.64	1.42 ± 0.69
Copepoda							
Copepoda	egg			0.17			
Acartia spp.	I-V	0.62 ± 0.40	0.26 ± 0.07	2.15 ± 0.95	0.6		
A. longiremis	I-VI	4.70 ± 1.83	1.19 ± 0.33	2.93 ± 2.00	4.85 ± 1.80		1.88 ± 0.62
Aetideidae	I-V		0.37	0.4	0.37	0.45	
Calanus spp.	I-VI	2.97 ± 1.64	0.30 ± 0.12	1.06 ± 0.13		0.86 ± 0.38	1.03
C. finmarchicus	I-VI	68.55 ± 14.36	21.73 ± 3.32	20.40 ± 1.71	92.58 ± 12.47	48.77 ± 7.04	65.95 ± 6.75
C. glacialis	III-VI	0.86 ± 0.30	0.17	0.28 ± 0.11		1.51 ± 0.49	1.38 ± 0.28
C. hyperboreus	III-VI	3.27 ± 0.92	2.07 ± 0.58	1.31 ± 0.37	3.80 ± 1.75	2.38 ± 1.05	3.00 ± 1.84
Centropages hamatus		17.01 ± 7.05	6.97 ± 2.01	1.59 ± 0.57	17.29 ± 5.99	1.41 ± 0.61	35.33 ± 9.93
Microcalanus spp.	VI		0.18	0.57			
Pseudocalanus spp.	II-VI	31.49 ± 4.71	28.98 ± 4.43	90.91 ± 12.08	63.99 ± 7.46	105.33 ± 13.80	119.11 ± 9.10
Paraeuchaeta norvegica	I-III, V		0.31 ± 0.16	0.47 ± 0.17	0.32 ± 0.05	0.43 ± 0.23	
Heterorhabdus spp.	I-V	0.53 ± 0.11	0.11 ± 0.06	0.25			
Metridia longa	I-VI	3.38 ± 1.02	10.62 ± 2.21	9.15 ± 2.61	10.20 ± 3.79	12.86 ± 2.12	15.50 ± 4.08
Scolecithricella minor	I-VI	0.25		0.13		0.48 ± 0.17	1.37
Eurytemora spp.	I-V					0.26	
E. herdmani	VI	0.38 ± 0.17					
Temora longicornis	I-VI	55.37 ± 20.87	19.69 ± 6.52	9.43 ± 5.59	313.49 ± 118.06	7.68 ± 2.24	189.18 ± 48.86
Tortanus discaudatus	I-VI	0.47	0.23 ± 0.03	0.47			

Oithona atlantica	VI	0.21	0.22 ± 0.05	0.48 ± 0.04	0.90 ± 0.17		
O. similis	I-VI	1.20 ± 0.40	1.66 ± 0.47	3.02 ± 1.08	3.47 ± 0.72	0.64 ± 0.10	1.52 ± 0.87
Triconia borealis	VI	0.17					
Harpacticoida						0.37	
Microsetella norvegica	I-V		0.17				
Cirripedia	larvae	0.21					
Euphausiidae							
Euphausiidae	egg	0.67 ± 0.22	0.04 ± 0.02	2.80 ± 1.46	0.15 ± 0.15	0.01	0.01
Euphausiidae	larvae	4.60 ± 1.58	0.16 ± 0.07	2.08 ± 1.42	1.13 ± 0.65	0.57 ± 0.20	0.33 ± 0.33
Thysanoessa raschii					0.37		
Invert egg		1.32					
Decapoda	larvae	0.97 ± 0.55	0.05	0.35	0.50 ± 0.23		
Chionoecetes opilio	zoea	0.38 ± 0.04					
Amphipoda	larvae					0.37	
Gammaridae			0.12	0.17			
Hyperiidae					0.56 ± 0.13	0.55 ± 0.26	0.72 ± 0.29
Themisto spp.					1.74		
T. compressa					0.6		
Isopoda	larvae	0.21	0.35				
Bivalvia			0.05				
Pteropoda		0.21					
Gastropoda		1.16 ± 0.51	4.74 ± 1.00	0.80 ± 0.18	18.54 ± 5.31	1.06 ± 0.17	14.72 ± 4.52
Gastropoda	egg	0.23 ± 0.02		0.25			
Bryozoa	cilie				7.29 ± 2.34		
Ophiura	larvae				4.11 ± 0.71		
Chaetognatha		0.69 ± 0.13	2.16 ± 0.63	0.38	1.93 ± 0.42	2.38 ± 0.44	4.67 ± 1.90
Larvacean		3.48 ± 1.44	1.98 ± 0.48	8.63 ± 4.73	2.33 ± 0.29		
Unidentified			0.11 ± 0.06				
Total plankton density		212.53 ± 52.26	104.17 ± 15.76	184.85 ± 37.37	550.62 ± 125.47	185.70 ± 22.33	447.07 ± 58.44

Table 3. Average station density (individuals m^{-3}) of all fishes sampled with the bongo nets, identified to the lowest possible taxonomic level (mean ± SE). All fish were pooled under "Teleost" for analysis.

		2017		2018		2019	
Species	Stage	Aug	Sept	Aug	Sept	Aug	Sept
Clupea harengus	larvae		0.01		0.01		0.01
Gadus morhua	larvae			0.01			0.01
Liparis spp.	larvae	0.01					0.01
Sebastes spp.	larvae			0.01			
Sebastes fasciatus	larvae	0.01					
Stichaeidae	larvae	0.01					0.01
Ulvaria subbifurcata	larvae	0.02					
Tautogolabrus adspersus	larvae	0.09 ± 0.05	0.01				
Mallotus villosus	larvae	0.31 ± 0.11	0.06 ± 0.01	0.05 ± 0.02	0.03 ± 0.01	0.08 ± 0.03	0.08 ± 0.02
Glyptocephalus cynoglossus	larvae	0.02					0.01
Limanda ferruginea	larvae	0.01					0.01

Table 4. Plankton genera (or next lowest taxonomic level available) that contributed greater than 5% to observed similarities (SIMPER) within cluster groups. The three most abundant genera of copepods (*Calanus*, *Pseudocalanus*, and *Temora*) were pooled.

Group	Species	Contribution (%)
A	*Calanus*	15.71
	Temora	15.37
	Pseudocalanus	14.35
	Evadne	11.07
	Acartia	9.07
	Larvacean	7.57
	Euphausiidae	7.56
	Oithona	5.81
B	*Pseudocalanus*	16.6
	Calanus	15.62
	Temora	11.17
	Metridia	9.70
	Evadne	8.14
	Gastropoda	6.92
	Oithona	6.30
	Acartia	6.27
	Larvacean	5.06
C	*Pseudocalanus*	19.48
	Calanus	15.48
	Metridia	15.01
	Ostracoda	7.25
	Larvacean	6.80
	Oithona	6.79
	Temora	6.55
	Paraeuchaeta	6.34
	Euphausiidae	5.37
D	*Temora*	14.55
	Calanus	13.31
	Pseudocalanus	12.13
	Gastropoda	8.15
	Metridia	6.52
	Evadne	5.72
	Oithona	5.59
	Acartia	5.47
	Larvacean	5.30
E	*Pseudocalanus*	24.39

	Calanus	20.67
	Metridia	14.06
	Temora	11.36
	Evadne	7.56
	Chaetognatha	5.62
	Oithona	5.40
F	*Pseudocalanus*	23.01
	Temora	22.59
	Calanus	19.75
	Gastropoda	10.72
	Metridia	*7.92*

Table 5. PERMANOVA results showing the variability in plankton communities attributed to environmental variables (primarily mean bottom water salinity) and temporal differences (included as the interaction term: YearMonth). P(perm) reflects the p-value calculated from test permutations (n=999).

Variables	p(perm)	Components of variation %
Environmental		
Surface temperature	0.001	7.7%
Bottom temperature	0.001	8.1%
Bottom salinity	0.001	44.7%
Surface salinity	0.001	12.8%
Factor: YearMonth	0.001	12.8%
Residual		13.9%

Table 6. Average isotope signatures of herring and potential prey items from August to November in 2018 and 2019. The average δ13C reflects the lipid-normalized values.

Year	Taxa	Month	N	δ^{15}N (‰) ± SE	δ^{13}C (‰) ± SE
2018	Herring	Aug	15	12.56 ± 0.05	-20.48 ± 0.11
		Sep	50	12.46 ± 0.05	-20.22 ± 0.10
		Oct	54	12.41 ± 0.06	-20.5 ± 0.09
		Nov	15	12.28 ± 0.09	-20.76 ± 0.10
	Ostracod	Sep	1	10.74	-18.38
	Copepod	Aug	5	10.19 ± 0.35	-19.47 ± 0.21
		Sep	7	10.00 ± 0.48	-18.21 ± 0.59
	Euphausiid	Aug	2	8.95 ± 1.35	-21.97 ± 0.32
		Sep	3	9.86 ± 0.43	-22.09 ± 0.19
	Decapod	Aug	2	9.46 ± 1.82	-19.86 ± 0.20
		Sep	2	8.98 ± 0.57	-21.54 ± 0.13
	Amphipod	Aug	1	9.26	-20.00
		Sep	5	9.78 ± 0.49	-20.63 ± 0.62
	Clione	Sep	1	7.70	-20.54
	*Limacina**	Aug	1	7.50	-11.98
		Sep	3	7.89 ± 0.34	-13.06 ± 0.79
	Fish egg	Aug	2	13.32 ± 1.84	-19.68 ± 0.41
2019	Herring	Aug	18	12.71 ± 0.09	-20.79 ± 0.03
		Sep	44	12.56 ± 0.04	-20.69 ± 0.04
		Oct	46	12.63 ± 0.04	-20.87 ± 0.05
	Ostracod	Aug	2	10.04 ± 0.54	-19.62 ± 3.83
	Copepod	Aug	4	9.82 ± 0.47	-20.90 ± 1.56
		Sep	11	9.20 ± 0.18	-21.55 ± 0.68
	Euphausiid	Aug	2	12.58 ± 2.08	-20.49 ± 0.65
		Sep	4	9.50 ± 0.29	-23.03 ± 0.36
	Decapod	Aug	2	11.60 ± 2.16	-21.33 ± 1.52
		Sep	2	8.89 ± 0.59	-23.06 ± 0.80
	Amphipod	Aug	6	10.92 ± 0.57	-21.58 ± 0.46
		Sep	11	9.54 ± 0.25	-22.35 ± 0.27
	*Limacina**	Aug	1	8.85	-13.93
		Sep	4	6.80 ± 0.08	-12.90 ± 0.8
	Chaetognath	Aug	3	11.36 ± 0.62	-22.01 ± 0.24
		Sep	4	11.97 ± 0.33	-22.65 ± 0.25
	Fish egg	Aug	4	12.94 ± 1.62	-20.83 ± 0.67
	Capelin	Sep	4	10.41 ± 0.24	-23.82 ± 0.16

* For *Limacina*, the δ^{13} C value was first corrected to remove the inorganic carbon (calcium carbonate shell) before the lipid-correction was applied.

2.6 Figures

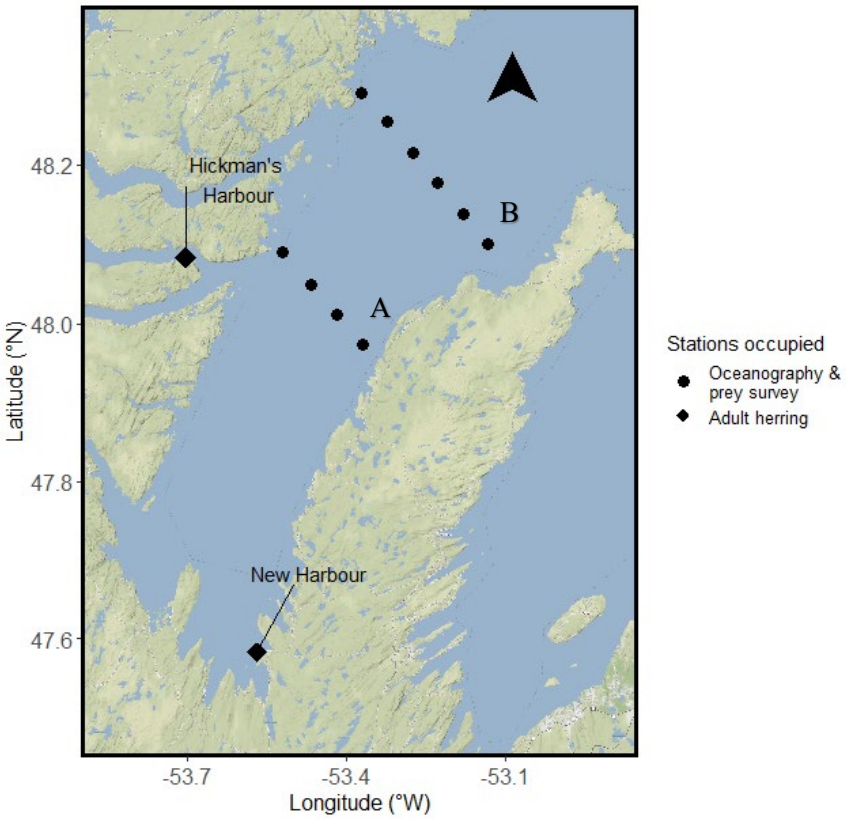

Figure 1. Map of the study site in Trinity Bay, Newfoundland, with circles denoting stations along two transects (A and B) that were sampled for temperature and salinity, and where bongo nets were deployed to collect zooplankton. Diamonds indicate where adult herring were sampled with gillnets.

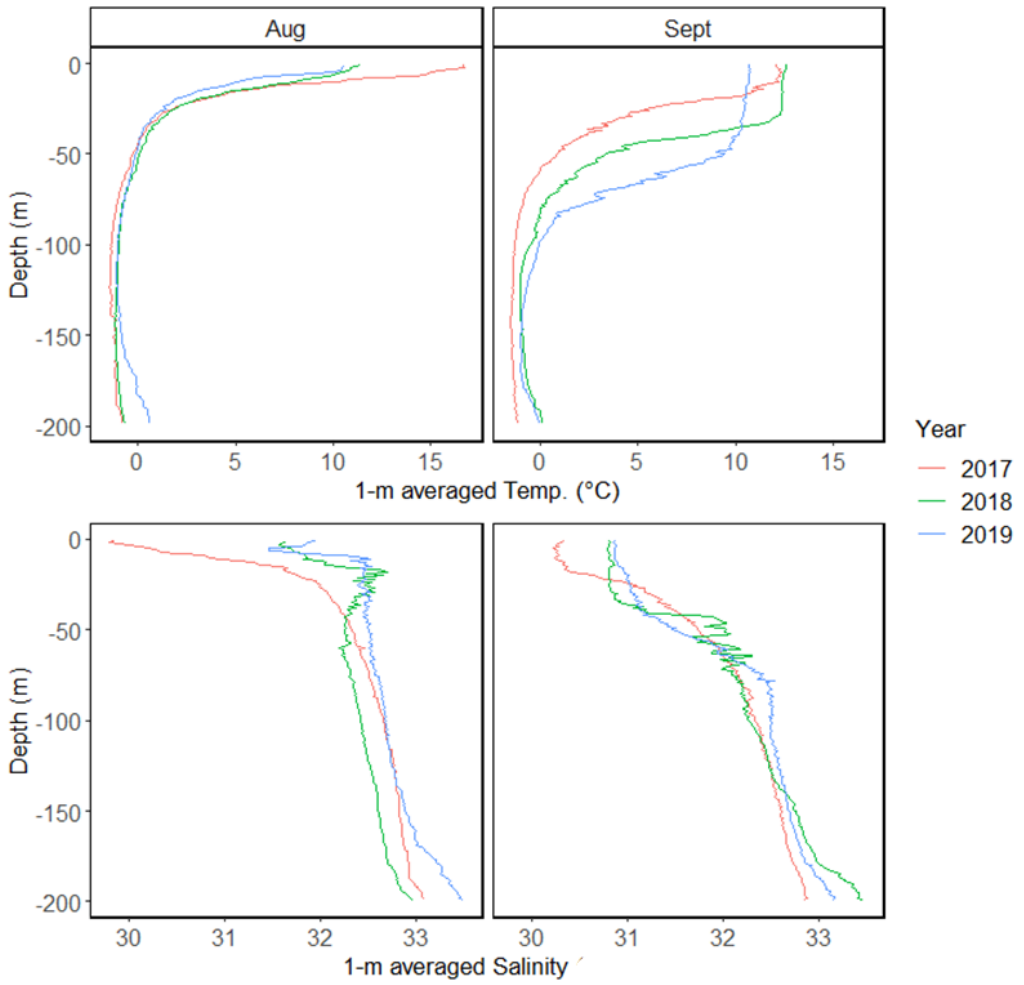

Figure 2. Temperature and salinity profiles in mid-August and mid-September of 2017 – 2019 with values averaged by 1-m depth intervals.

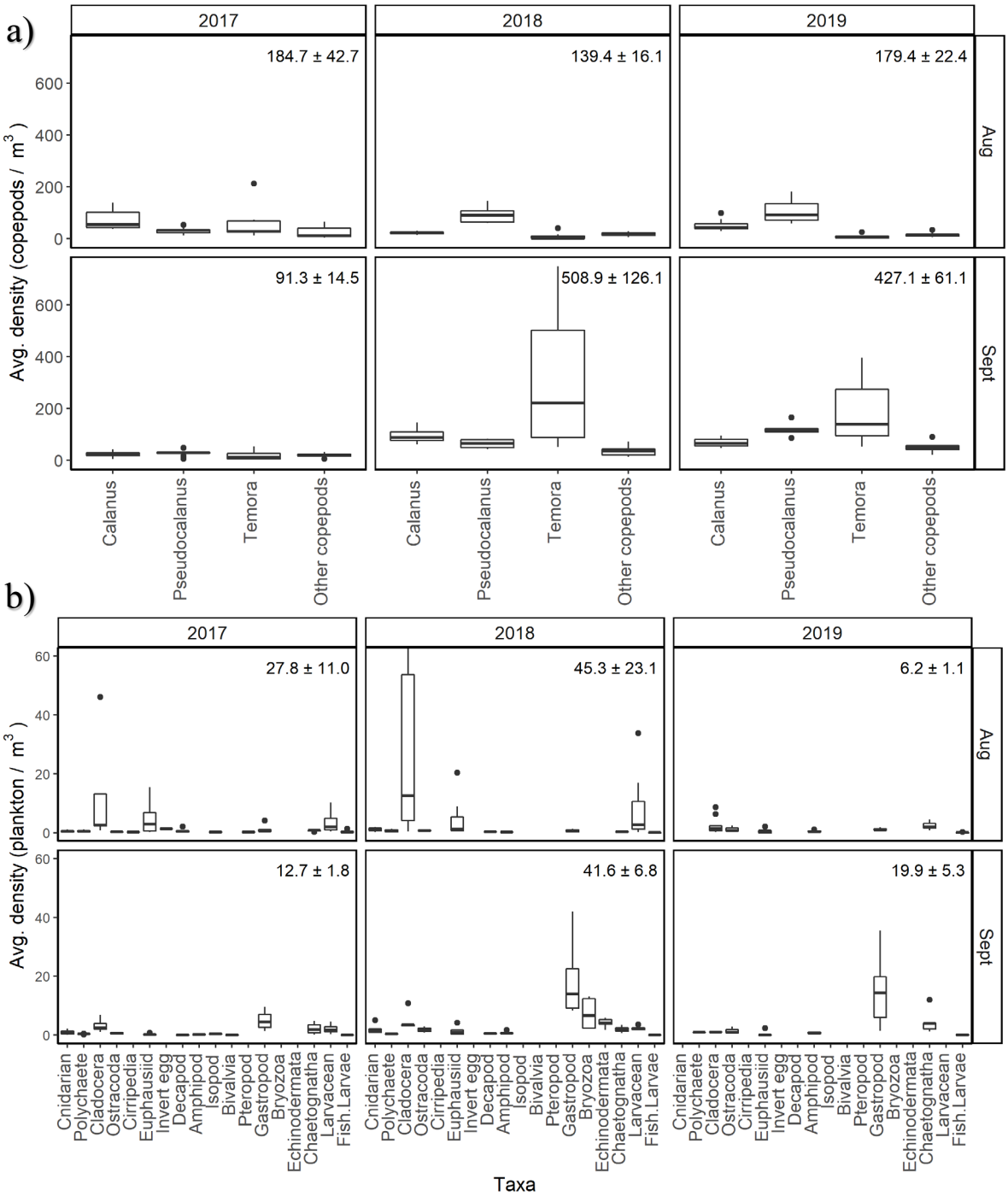

Figure 3. Average station density of plankton groups collected by survey with estimated total density and SE reported in the upper right of each plot. Boxplots display the median with lower and upper box hinges representing the 25th and 75th quantiles, respectively. Whiskers represent either the minimum/maximum value or 1.5 * interquartile range. a) Density of three dominant copepod and the pooled value of all 'Other' copepod genera, b) Density of all non-copepod groups. Data not depicted (3b) to preserve scale: one outlier in Aug 2017 (77.6 Cladocera/m^{-3}) and upper whisker in Aug 2018 (115.7 Cladocera/m^{-3}).

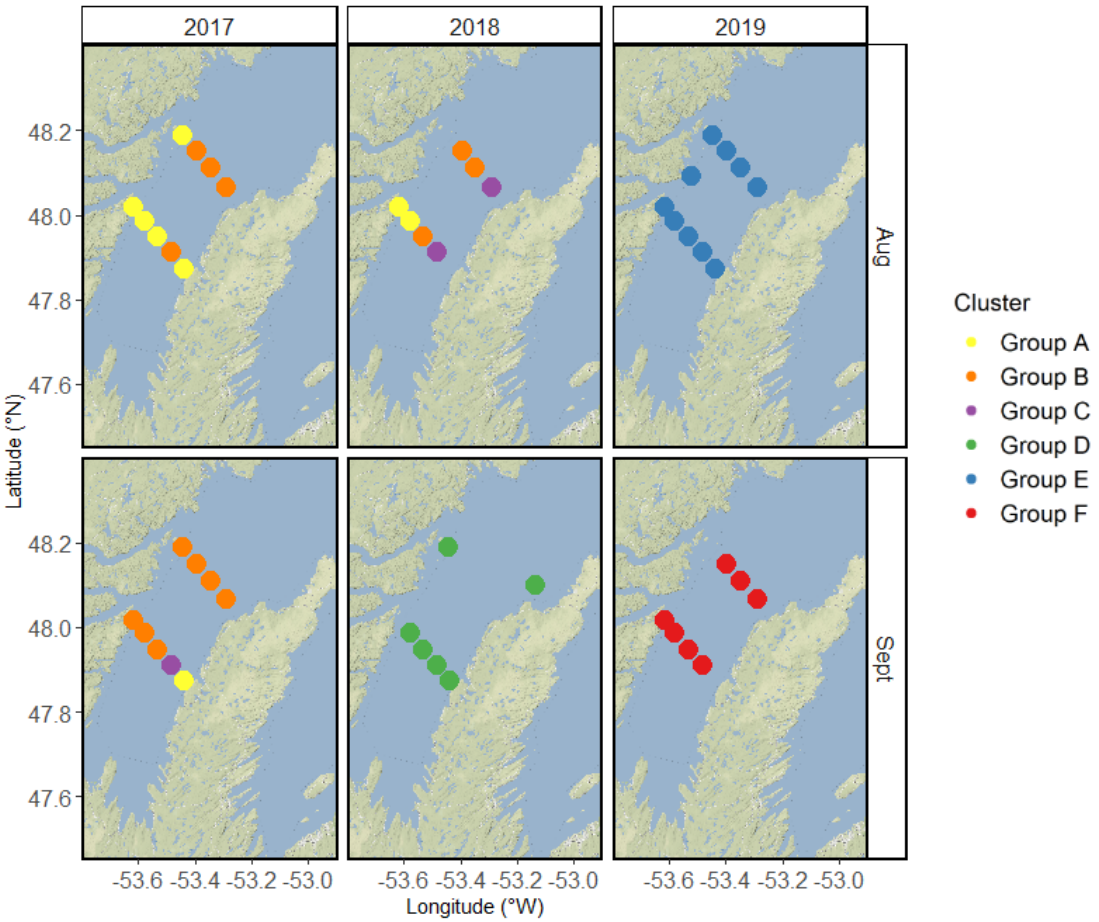

Figure 4. Cluster groups identified across zooplankton communities sampled from 2017-2019, defined by Bray-Curtis similarity index and cluster analysis with a 72% cutoff.

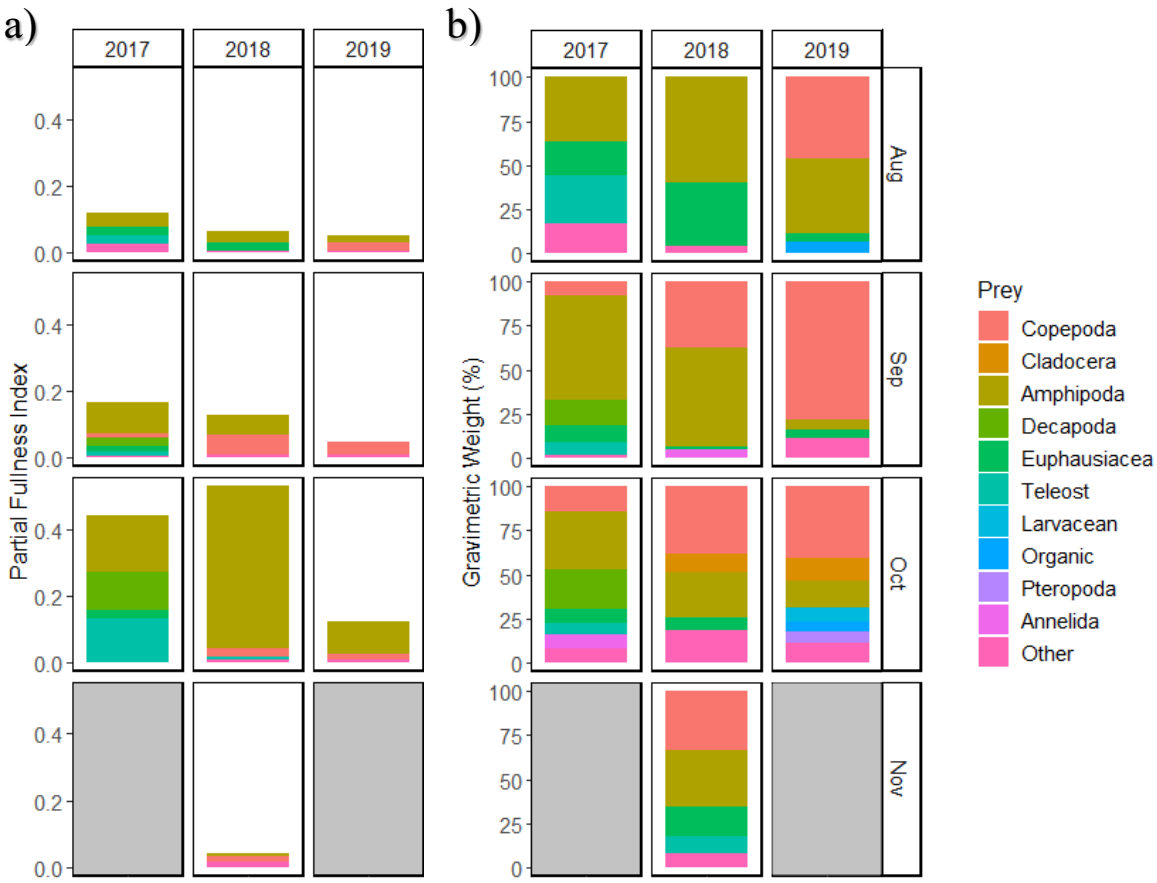

Figure 5. Weight-based diet analyses of prey item contribution by a) partial fullness index, b) gravimetric weight. Prey items that contributed < 5% to gravimetric weight were pooled as 'Other'. No sampling was conducted in November 2017 and 2019 (grey boxes).

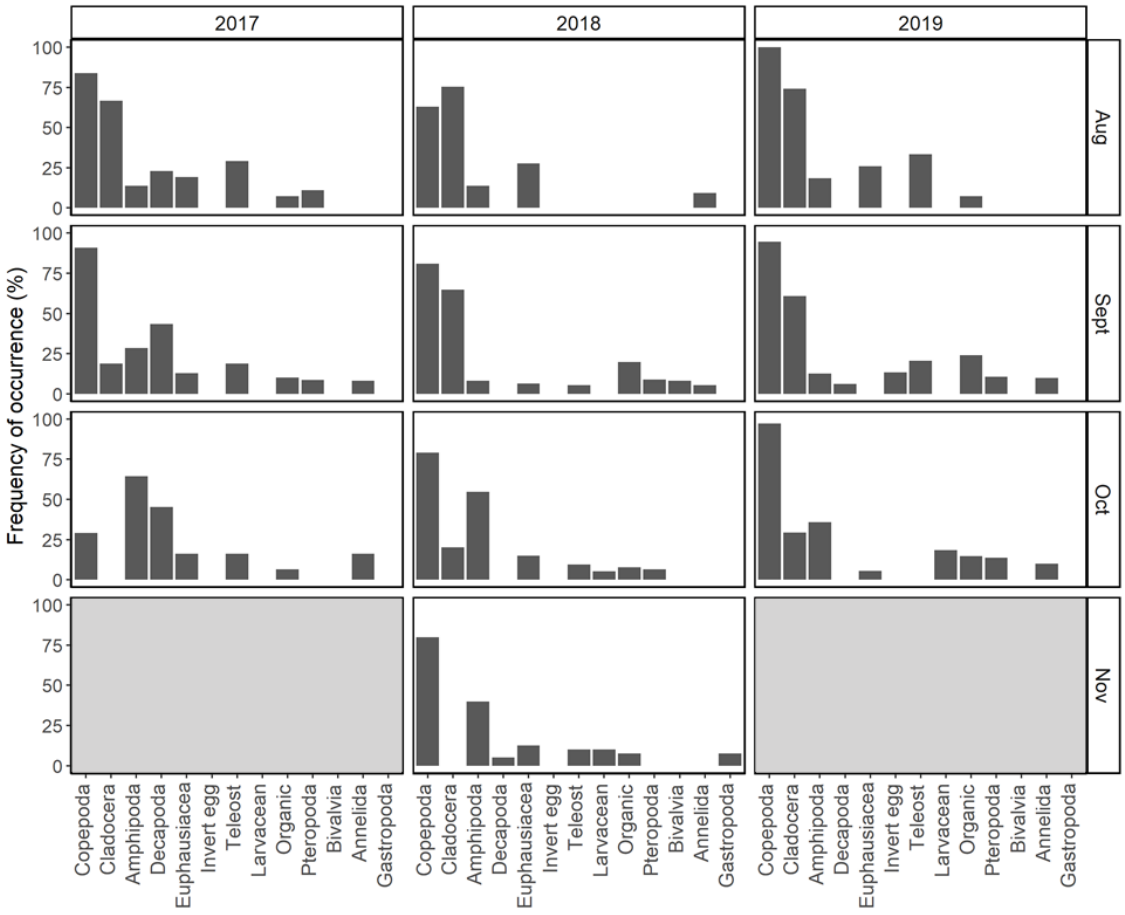

Figure 6. Frequency of occurrence of each prey category in herring diets by month and year. Only prey categories with >5% frequency for a given month were included. No sampling was conducted in November 2017 and 2019 (grey boxes).

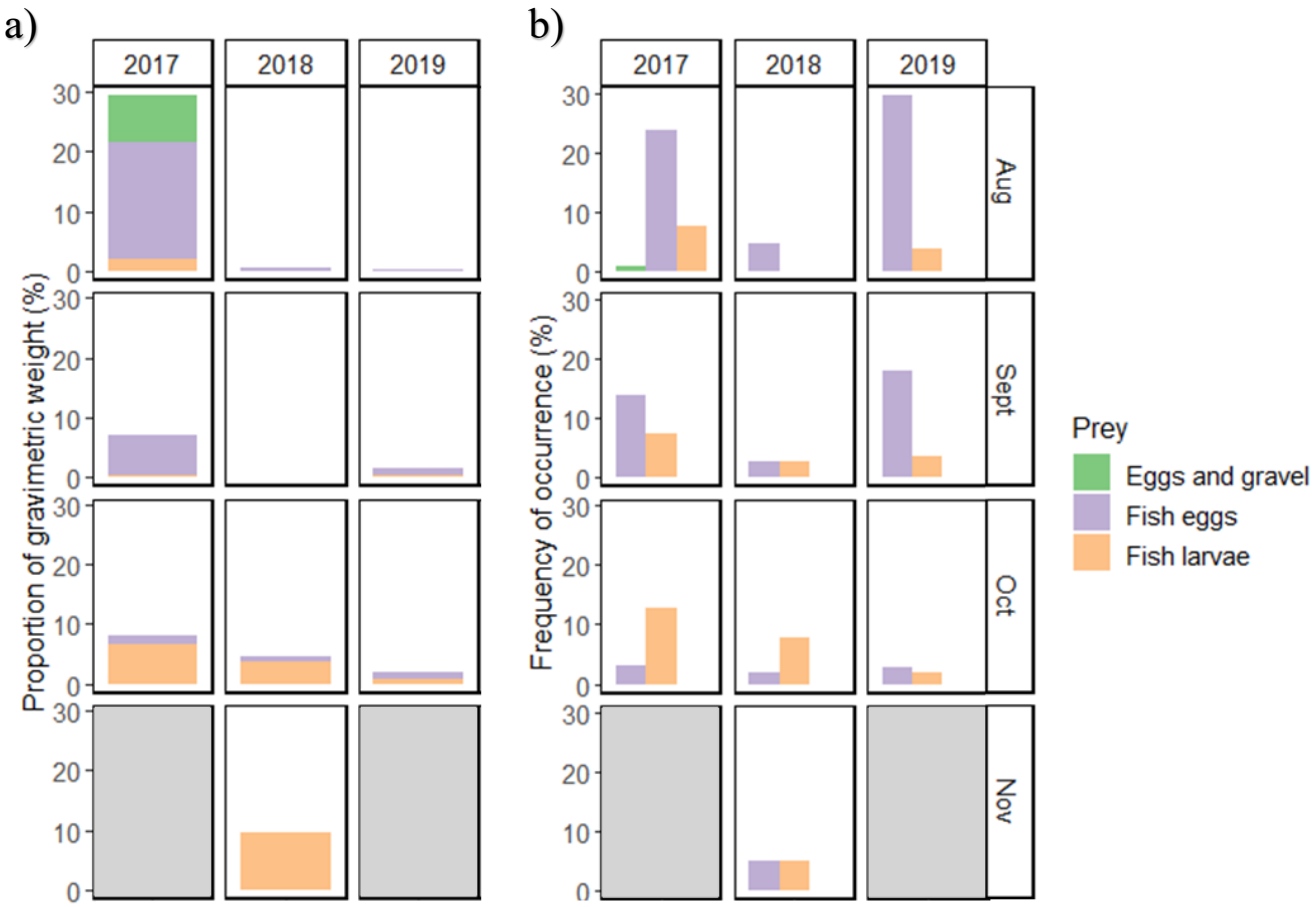

Figure 7. Presence of fish in the diets of herring represented by a) gravimetric weight and b) frequency of occurrence. 'Eggs and gravel' indicate benthic, adhesive eggs (likely capelin) that could not be separated from sediments. The category 'Fish larvae' includes all remnants of fish identified in the stomach contents. No sampling was conducted in November 2017 and 2019 (grey boxes).

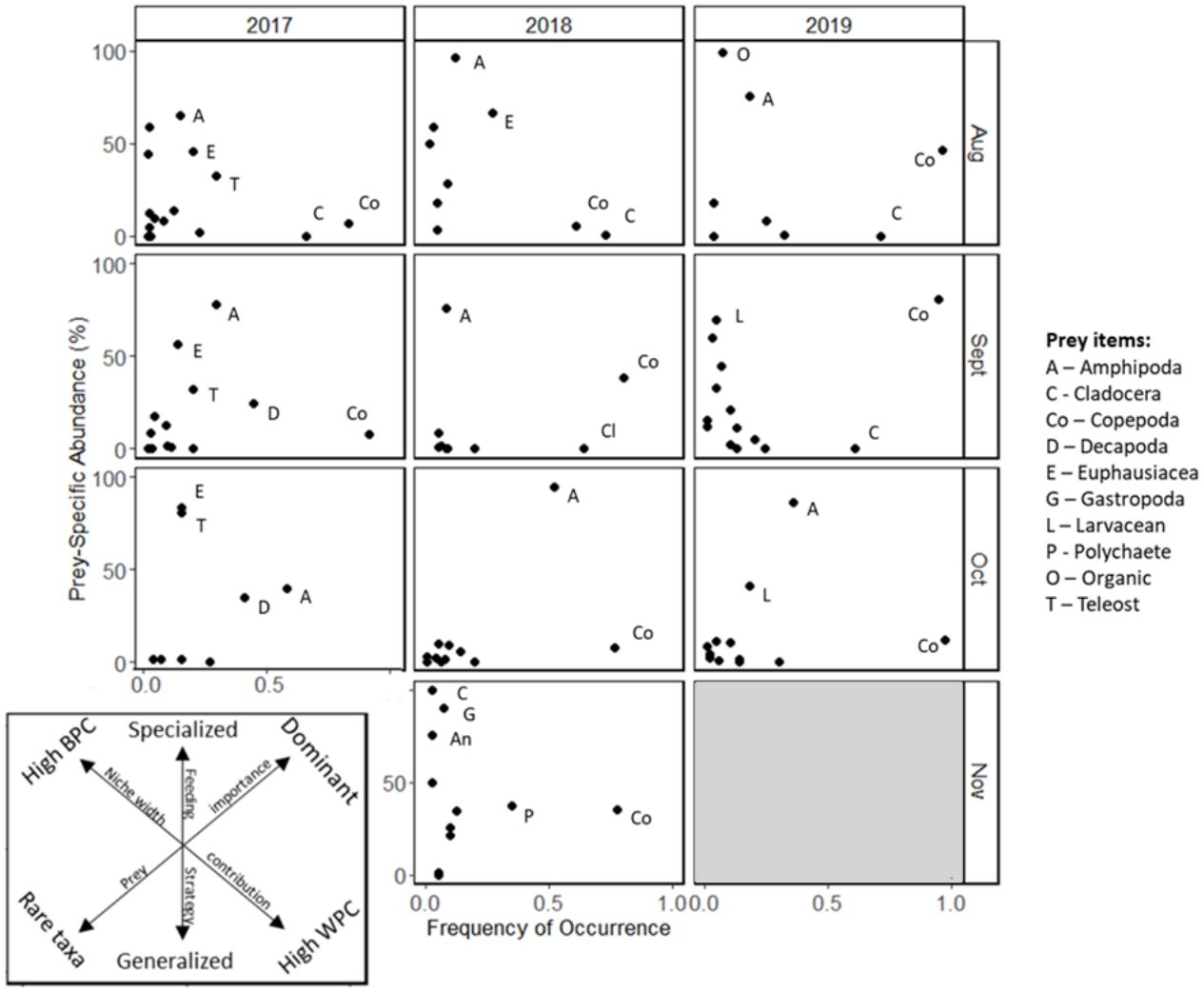

Figure 8. Prey-specific abundance (%) relative to the frequency of occurrence for all prey items in herring stomach contents, with key taxa identified. The explanatory axes in the bottom-left inset depict the foraging patterns described by Costello (1990) with modifications by Amundsen et al. (1996). The vertical axis reflects feeding strategy (prey preferentially consumed vs. generalized feeding), prey importance, and niche width contribution, differentiated as between-phenotype contribution (BPC; individuals specialized on different prey items) and high within-phenotype contribution (WPC; individuals exhibiting generalized feeding on common prey items). No sampling was conducted in November 2017 and 2019.

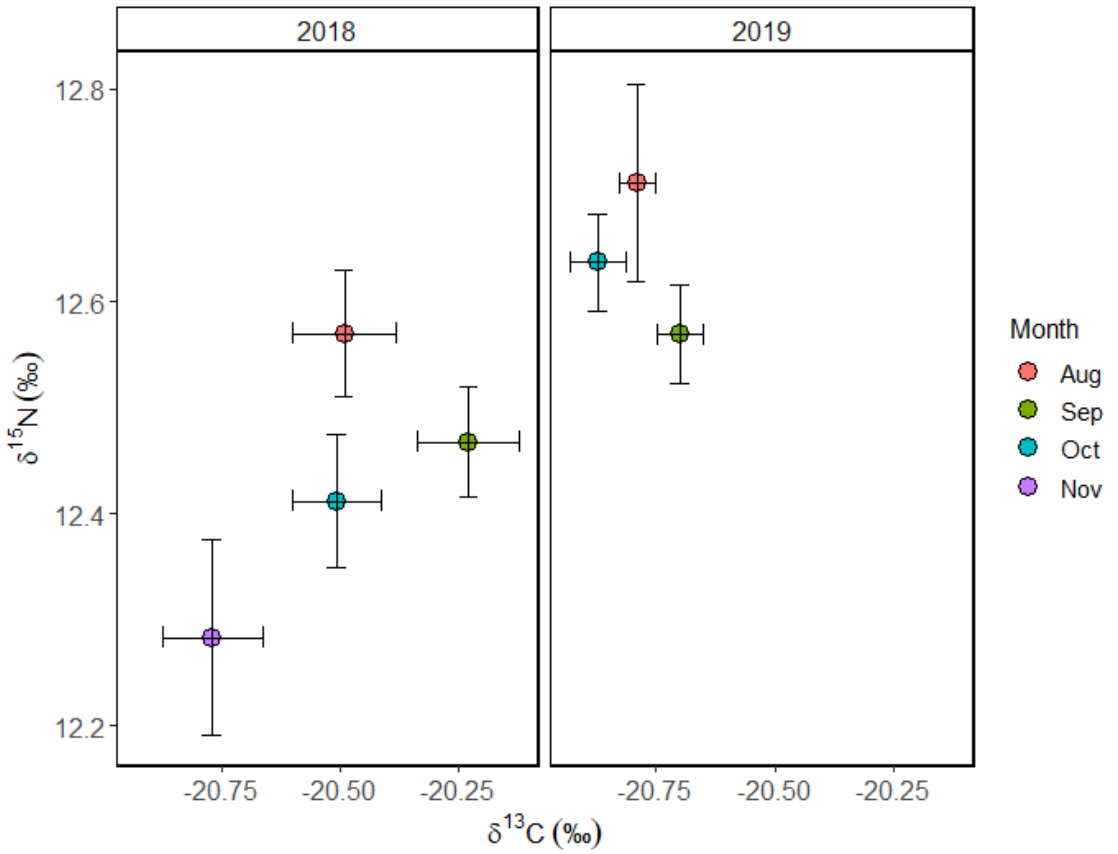

Figure 9. Mean nitrogen and lipid-normalized carbon delta values (± SE) of herring collected in August and September of 2018 and 2019.

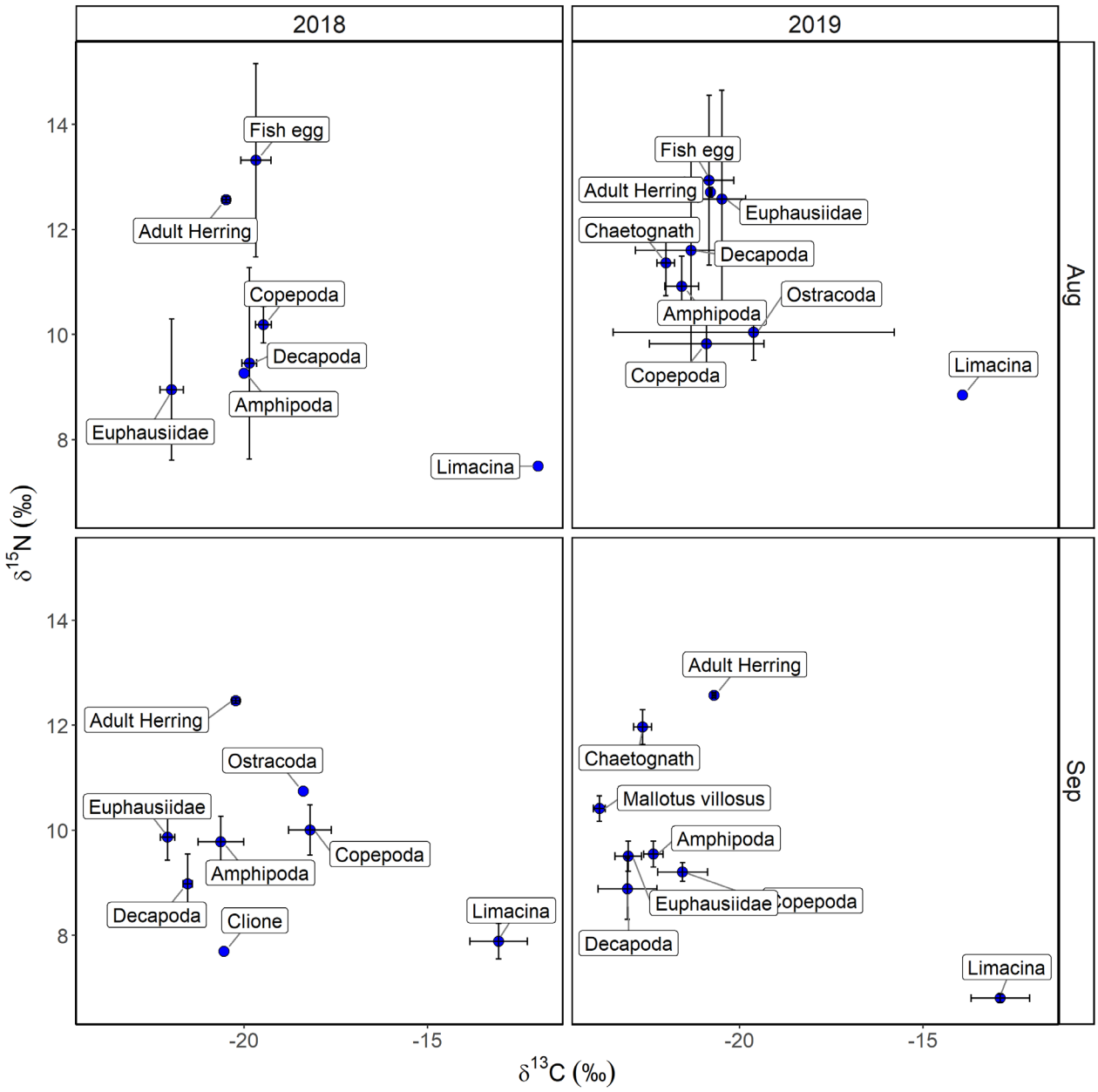

Figure 10. Biplot of nitrogen and lipid-normalized carbon signatures (mean ± SE) of herring and al prey items collected in August and September of 2018 and 2019. Values without error bars reflect occurrence of prey items with the exception of adult herring, which have low SE values.

Chapter three: Summary

3.1 Herring and climate change

By the end of this century, sea surface temperatures (0-100m) are estimated to increase by 0.6°C to 2.0°C (relative to 1850-1900; Collins et al. 2013), with the fastest warming temperatures observed in the Arctic and sub-Arctic seas (IPCC 2014). Although climate change models vary in the degree of warming the North Atlantic will exhibit in the coming decades (Saba et al. 2016), there is general agreement that surface waters will warm and freshen in response to increasing sea ice melt (primarily north of 45°N), and there will be increased stratification and reduced convection, which may alter circulation patterns in the study area (Alexander et al. 2020). Relative to the 1960s, the assemblages of calanoid copepods in the Northeast Atlantic have exhibited concurrent range contractions of Arctic species (e.g., *Calanus glacialis*) and range expansions of sub-Arctic species (e.g., preferred herring prey item *Calanus finmarchicus,* Darbyson et al. 2003) to the north (Beaugrand et al. 2009). Similarly, subtropical and warmer-water species have also been documented farther north than previous range distributions, the latter extending from 52° to 62°N in under half a century (Beaugrand et al. 2009). Variation in temperature has also prompted changes in fish populations in the latter half of the 20th century, such as a northward shift in the distribution range of numerous species (Cheung et al. 2013) as well as dramatic fluctuations in spawning stock biomass of Norwegian spring-spawning herring (Toresen and Østvedt 2000).

In the Northwest Atlantic, the planktivore functional group (capelin, sand lance, herring) is projected to lose a significant amount of realized thermal habitat from their current distribution by 2030, with both capelin and sand lance fairing among the worst of the 46 species evaluated (Shackell et al. 2014). Herring may be less susceptible to changes in temperature (Shackell et al. 2014). Furthermore, herring may be more appropriately classified in the zoopiscivore functional group, as demonstrated in this study, which may lessen the projected impacts of habitat loss due to climate change (Shackell et al. 2014). Herring may be particularly well suited to expand their distribution north, even potentially cross into Pacific waters as the Northwest Passage warms (Wisz et al. 2015). While this assertion is primarily based on fecundity and larval dispersal estimates (Wisz et al. 2015), the northward expansion of key prey items such as *Calanus finmarchicus* (Beaugrand et al. 2009) may further improve the likelihood of herring successfully colonizing northern habitats under future warming scenarios.

The biocomplexity of herring stocks adaptive foraging strategy (Gibson and Ezzi 1992) may potentially increase herring resilience to climate warming in the Northwest Atlantic. The dominant spawning phenology is largely driven by environmental conditions, which historically varied along a latitudinal gradient, and as temperatures warmed in the late 1990's and early 2000's, fall-spawners became increasingly dominant in the northern stocks (i.e.; Gulf of St. Lawrence and eastern Newfoundland; Melvin et al. 2009). My findings further support this trend, with nearly 75% of all herring collected belonging to the fall-spawning component. Nye et al. (2009) found that herring populations were able

to adapt to fluctuations in oceanographic conditions, including recent climate warming, and, consequently, herring exhibited the largest change (increase) in area occupied of the 36 stocks studied over a 40-year time series. If conditions continue to warm, this may lead to an overall reduction or loss of herring phenotypic plasticity as spring-spawning sub-populations continue to decline in abundance (Melvin et al. 2009). Furthermore, the timing of spawning has a genetic link (Lamichhaney et al. 2017), which may further reduce regional herring biocomplexity if climate conditions are unfavorable for spring-spawners. In Newfoundland, the adaptive capacity of herring populations, as well as experiencing low levels of exploitation, may explain why herring populations did not collapse with capelin and groundfish stocks in the early 1990s. However, it is unclear if this apparent resilience of herring stocks in Eastern Newfoundland will persist given the loss in biocomplexity.

3.2 Reflections on methodology

Oceanography and prey field analysis

The original scope of this thesis was focused on describing the late summer and fall diets of adult herring through field collections and stomach content analyses. While the ichthyoplankton data were an original component of the project to evaluate the larval prey field available to herring, using the ichthyoplankton samples to also provide zooplankton prey field data and the stable isotope project were additional research components that were opportunistically added to enhance the thesis. I included these data sources to provide a greater ecosystem context for the herring diet data by relating diets to the available prey

field. However, this posed a unique challenge to integrate projects designed independently into the central thesis. Ichthyoplankton surveys have been conducted annually since 2002 to assess larval capelin abundance (Murphy et al. 2018). While bongo nets are readily used in plankton collection (McGowan and Brown 1966; Cowen et al. 2013), the gear does not perform well for more mobile nekton capable of evading the nets (e.g., larger larval or transformation stage fishes) or benthic species (e.g., euphausiids). Many zooplankters perform diel vertical migration at night, rising to the surface waters to feed under cover of darkness (Hays 1996). Plankton tows for this study were conducted exclusively during the day, which may result in an overall underestimation of plankton densities and particularly low estimates for benthic-associated taxa (e.g., euphausiids, amphipods; Shaw and Robinson 1998). Nonetheless, the sampling protocol was consistent among surveys which ensured this potential bias was uniform across months, and both amphipods and euphausiids were present in the bongo net samples so trends in abundance between surveys were still detected.

In terms of diet analysis approaches, ideally, enumeration of all prey items individually and a volumetric estimate of each (collective) prey item would have been obtained (Hyslop 1980). This would have expanded the analyses that were applicable to this diet dataset (e.g., Index of Preponderance, Natarajan and Jhingran 1962; Index of Relative Importance, Pinkas et al. 1971) but would have added considerable processing time even with the support of several technicians. Additionally, the aforementioned approaches have well-described limitations and can introduce biases (Hyslop 1980; Baker et al. 2014). By using

measures of diet contribution by weight (gravimetric and partial/total fullness indices) as well as prey presence (frequency of occurrence), I sought to achieve a balance of increased sampling effort and obtaining sufficient data to evaluate the summer and fall diet of herring so I chose simple but robust data analyses methods (Baker et al. 2014). To investigate feeding strategy, I only used herring diet data instead of traditional selectivity indices that require concurrent sampling of the environmental prey field (e.g., Manly-Chesson index, Index of electivity; Confer and Moore, 1987), so I was able to assess prey selectivity independent of the prey field samples (Amundsen et al. 1996).

Stable isotope analyses

Quantitative applications of the stable isotope analysis were limited by the narrow range of prey items collected. When present in the samples, larvaceans and all life stages of fishes produced insufficient weights after freeze-drying and could not be incorporated into the analysis. There was also a lack of representation of samples from the base of the food web, including phytoplankton and particulate organic matter. These samples would have helped provide a basis for distinguishing different sources of carbon in the ecosystem (Post 2002; Sokolowski et al. 2014). Although several small rivers feed into Trinity Bay, the overall input of freshwater (and thus, terrestrial sources of carbon) is thought to be minimal (Sheldon et al. 2015), but this has not been assessed. Additionally, the variation in carbon ratios of prey items reflects potential differences of carbon sources within the ecosystem, as shown by the enriched $\delta^{13}C$ of both *Limacina* and *Clione* pteropods relative to the depleted $\delta^{13}C$ of other prey items. I suggest further investigation of the lower trophic level

stable isotope signatures, particularly primary producers and particulate organic matter, to further inform the food web dynamics of Trinity Bay.

3.3 Future work

This work provides the first baseline description of late summer and fall adult herring diets in Trinity Bay. I found that diet is influenced by zooplankton composition and abundance, which in turn is influenced by fluctuations in the transport of Atlantic and Arctic waters into the bay by the Labrador Current (Sheldon et al. 2015). While most other bays in the region will also be influenced by the inshore branch of the Labrador Current (Pearce et al. 2014), each area will be influenced by a suite of factors (e.g., wind, freshwater input, bathymetry) which may support different zooplankton communities. I found that piscivory is an important component of adult herring diet, which has currently unknown consequences on the recruitment of commercial and non-commercial fish stocks in the NW Atlantic.

Throughout eastern Newfoundland, the degree of the shift in spawning phenology from predominately spring- to fall-spawning is variable with areas like Fortune Bay still predominantly comprised of spring-spawners (Bourne et al. 2018). Although the drivers of this shift in spawning are unknown, it has been suggested that a more abundant fall plankton bloom may produce improved feeding conditions for fall-spawned herring larvae (Wilson et al. 2018). If changes at the lower trophic levels were driving the shift in spawning phenology, it is reasonable to suggest that these differences may also vary among

bays, which may explain the differences in spawning component ratios between herring stocks.

Future research to address these questions should include an increase in spatial and temporal diet analyses (i.e., diet data of both juveniles and adults from all stock complexes in all seasons), increased inshore zooplankton sampling, particularly focused on macrozooplankton like amphipods and euphausiids, and increased ichthyoplankton sampling to assess the impact of juvenile and adult herring predation on larval survival and subsequent recruitment.

In addition to expanding herring diet analyses spatially and temporally, and considering both juvenile and adult herring, a comprehensive stable isotope analysis of all trophic levels within the bay, from primary producers to top predators, would provide an ecosystem context to the herring diet analyses. By limiting the scope of our analysis to herring as the top predator, I was not able to place herring signatures within the broader ecosystem. A broader ecosystem-based study would provide greater context for the trophodynamics in Trinity Bay and the northeastern coast of Newfoundland. Additionally, these results could then be compared to the Newfoundland Shelf ecosystem (Sherwood and Rose 2005; Krumsick and Fisher 2019), expanding on previous work which specifically examined Atlantic cod stable isotopes both inshore and offshore (Sherwood et al. 2007), and potentially may be useful to help resolve the extent of coastal zooplankton species being transported into Trinity Bay. I also suggest future stable isotope studies on herring diets

incorporate both sampling of herring and prey items in the offshore environment. By sampling herring during this phase of their migration, it would be possible to determine if there are diet differences between open ocean and coastal feeding.

To conclude, I propose that future work should explore variations in adult herring diet between offshore and nearshore habitats, winter and springtime diets in the bays, and assess the diet and selectivity of juvenile herring. Efforts to gain a more comprehensive understanding of herring in eastern Newfoundland will create a strong foundation for broader ecosystem studies. Critical goals, such as anticipating how ecosystems will respond to changes in climate and efforts to move towards an ecosystem-based management strategy, require a clear understanding of how species interact. This study provides key diet data for an understudied forage fish species in the NL ecosystem, which can be incorporated into both species-based and ecosystem modeling. Using data generated by stomach content analyses of commercial fish species sampled offshore during DFO's spring and fall multispecies surveys, Ecopath models have been developed for the Scotian Shelf (Bundy 2005) as well as along the Newfoundland shelf region (Tam and Bundy 2019). Diet data for herring are particularly useful as the species is rarely sampled in the offshore multispecies surveys due to its primarily coastal distribution. Diet data provides indicators of ecosystem resilience, trophic structure, and functionality (Tam et al. 2017). For the Newfoundland shelf region, which experienced a likely regime shift in the late 1980s (deYoung et al. 2004; Pedersen et al. 2017) and the simultaneous collapse of capelin,

a key forage fish species (Buren et al. 2014), it is essential to understand herring trophic ecology to assess how the ecosystem responds to an alternative dominant forage fish.

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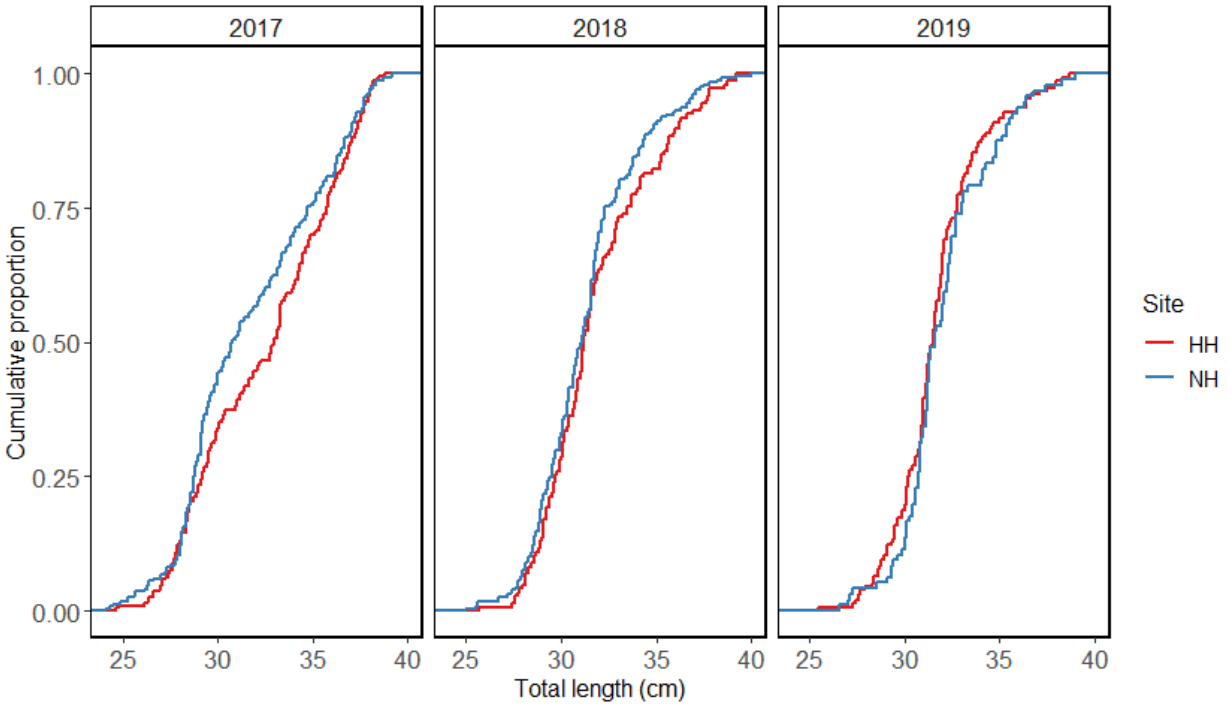
Appendices

Appendix A. Guide for maturity stages of herring used by Fisheries and Oceans Canada, St. John's, adapted from Parrish and Saville (1965) with input from B. Squires (pers. comm.). After completing spawning, herring are classified as Stage VIII (Spent) then revert to Stage III as they prepare to spawn the next year.

Maturity stage	Classification	Male description	Female description
I	Immature	Testes small, threadlike, whitish or grey-brown	Gonads small 2-3 mm width, ovaries dark red
II	Early maturation	Testes width 3-8 mm width, reddish grey in color	Ovaries width 3-8 mm, eggs only visible under a microscope
III	Maturing/pre-spawning	Testes occupy half of ventral cavity, 1-2 cm width. Reddish grey in color	Ovaries occupy half of ventral cavity, width 1-2 cm. Eggs distinguishable with naked eye, orange in color
IV	Ready to spawn	Testes nearly length of body cavity. Testes white	Ovaries fill body cavity, yellow in color. Eggs are large, some transparent but not actively flowing
VI	Actively spawning	Testes ripe, milt flows freely	Ovaries ripe, eggs transparent and flow freely
VIII	Spent	Testes firm and larger than Stage II. Walls of testes are striated, blood vessels prominent. Dark red in color	Ovaries firm and larger than Stage II. Eggs not visible to naked eye. Ovary walls striated, dark red in color



Appendix B. Cumulative length-frequency curves for herring collected in each year of the survey from both field sites: HH – Hickman's Harbour and NH – New Harbour. No significant difference in length was found between sites.

Appendix C. List of all zooplankton collected from August through November in 2017, 2018, and 2019, identified to the lowest taxonomic level possible. Zooplankton that were found exclusively in the bongo net samples are denoted by a single asterisk (*) while zooplankton only identified in herring stomach samples are denoted by a double asterisk (**). Taxa that were found in both sampling methods have no notation.

Phylum CNIDARIA
Cnidaria

Phylum ANNELIDA
Class Polychaeta
Nereis spp.**

Phylum ARTHROPODA
Subphylum Crustacea
Order Cladocera
Evadne spp.
Podon spp.
Class Ostracoda
Subclass Copepoda
Order Calanoida
Acartia spp. *
A. longiremis *
Aetideidae
Calanus spp.
C. finmarchicus *
C. glacialis *
C. hyperboreus *
Centropages spp. **
*Centropages hamatus**
Microcalanus spp. *
Pseudocalanus spp.
Paraeuchaeta spp. **
P. norvegicus *
Heterorhabdus spp. *
H. norvegicus *
Metridia spp.
M. lucens
M. longa **
Paracalanus parvus **
Anomalocera patersoni **
Anomalocera spp. **
Scolecithricella minor *
Eurytemora spp. *

E. hermandi *
Temora spp. **
T. longicornis *
Tortanus discaudatus *
Order Cyclopoida
Oithona spp. **
O. atlantica *
O. similis *
Triconia borealis *
Order Harpacticoida
Class Maxillopoda
Cirripedia (larvae)
Class Malacostraca
Order Mysida (zoea – larvae) **
Order Euphausiacea
Euphausiidae (egg – nauplii *, calyptopis-furcilia)
Meganyctiphanes norvegica **
Thysanoessa raschii
Thysanoessa spp. *
Order Decapoda (zoea, megalope)
Chionoecetes opilio (zoea) *
Order Amphipoda
Caprellidae **
Eusirus cuspidatus **
Gammaridae
Hyperiidae
Hyperia spp. **
Hyperia galba **
Hyperia / Hyperoche spp. **
Hyperoche spp. **
Hyperoche medusarum **
Themisto spp.
T. abyssorum **
T. compressa
T. libellula **
Order Isopoda
Order Cumacea **

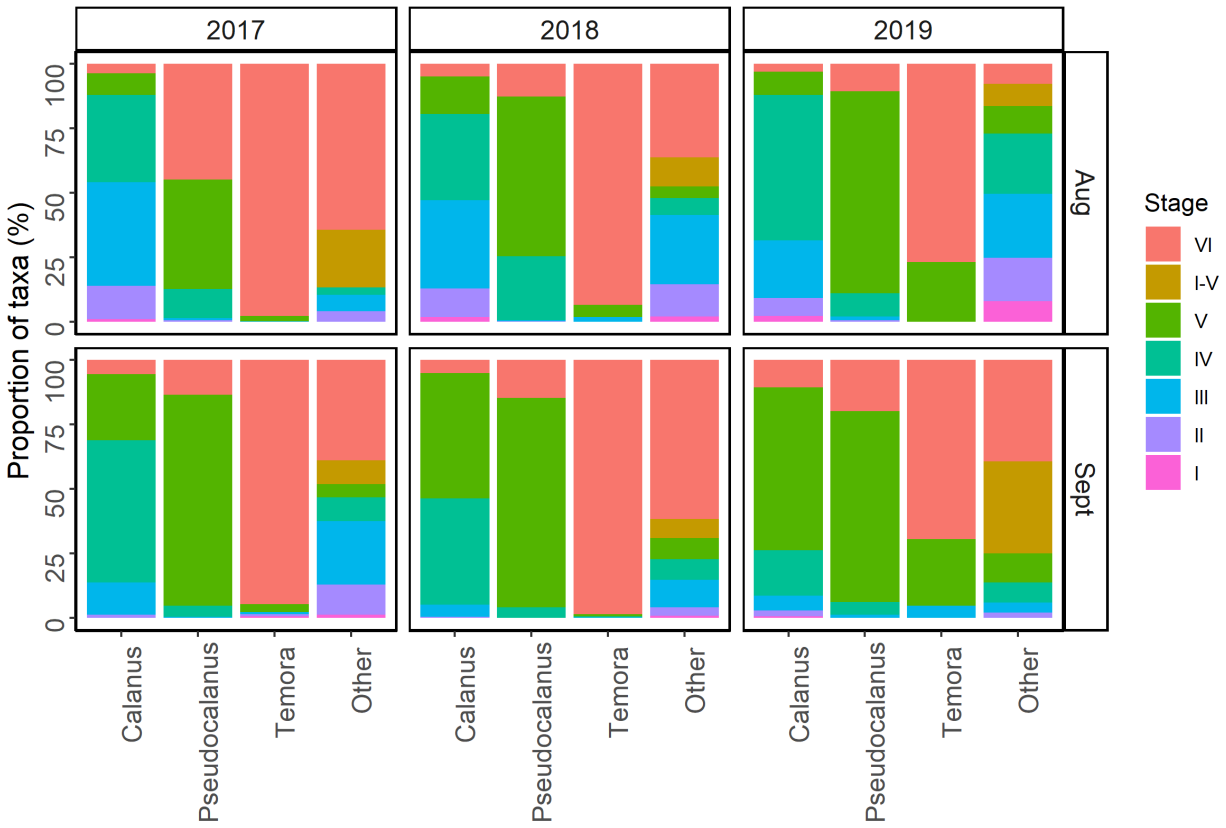
Phylum Mollusca
Class Bivalvia
Class Gastropoda (egg)
Order Pteropoda
Limacina spp. **
Clione spp. **

Phylum BRYOZOA *

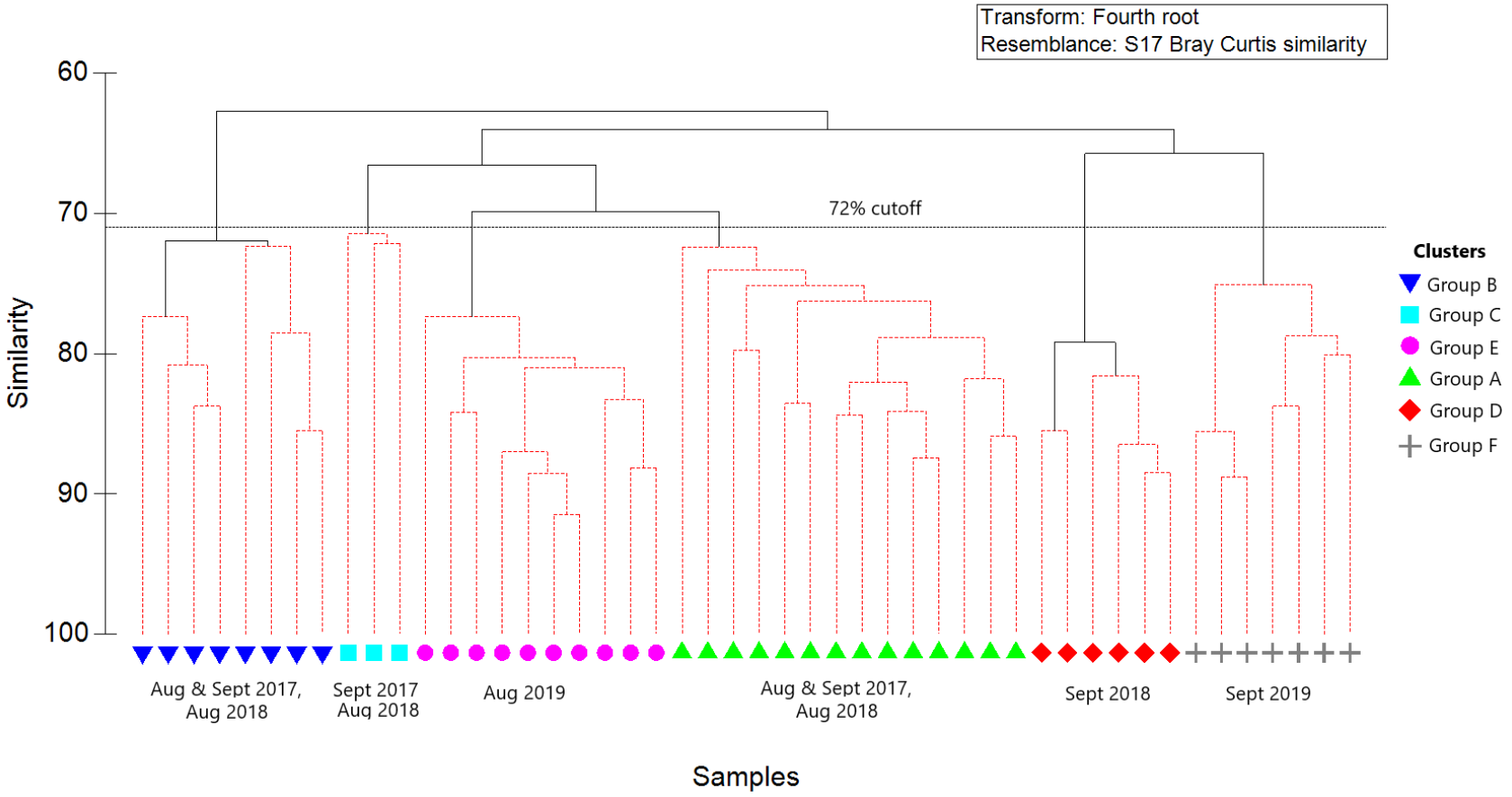
Phylum ECHINODERMATA
Class Ophiuroidea (larva) *

Phylum CHAETOGNATHA

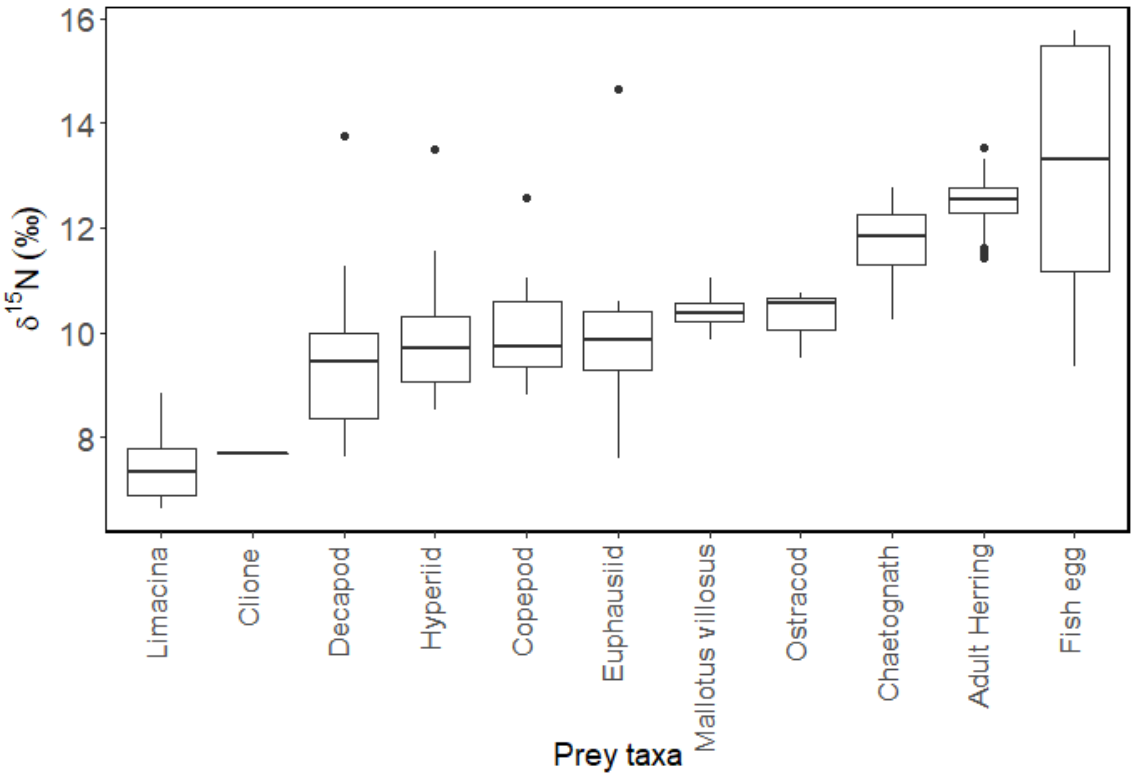
Phylum CHORDATA
Class Appendicularia (Larvacean)
Class Actinopterygii
Infraclass Teleostei (Fishes: larvae, age-1, otoliths)
- Clupeiformes
  - *Clupea harengus* *
- Gadiformes
  - Gadidae **
    - *Boreogadus saida* **
    - *Gadus morhua* *
- Scorpaeniformes
  - *Liparis* spp. *
  - *Sebastes* spp. *
  - *Sebastes fasciatus* *
- Perciformes
  - Stichaeidae
    - *Leptoclinus maculatus* **
    - *Ulvaria subbifurcata* *
- Labriformes
  - *Tautogloabrus adspersus* *
- Osmeriformes
  - *Mallotus villosus*
- Pleuronectiformes
  - *Glyptocephalus cynoglossus* *
  - *Limanda ferruginea* *
  - *Scophthalmus maximus* *



Appendix D. Proportion of top three genera of copepods in each stage of development with stages I-V representing copepodites and VI representing adults. All other copepods identified were collectively pooled as 'Other' and contained individuals that were only staged as copepodites (I-V).



Appendix E. Cluster analysis of stations across all months and years of sampling. The horizontal dashed line shows the 72% cutoff used to distinguish between cluster groups.



Appendix F. Mean nitrogen ratio of all prey taxa pooled across surveys, reflecting a spread of N^{15} ratios, likely encompassing multiple trophic levels. Boxplots display the median with lower and upper box hinges representing the 25^{th} and 75^{th} quantiles, respectively. Whiskers represent either the minimum/maximum value or 1.5 * IQR (interquartile range).

Appendix G. Summary of herring samples by month separated by spawning component (n=784). SpR: fall to spring-spawner ratio, FI: feeding incidence (stomach containing prey:total stomachs), TFI: total fullness index, TL: total length

		Fish collected		Feeding Incidence		Total Fullness Index		Total Length		Age		Maturity	
	SpR	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring
Aug-17	6.63	252	38	0.89	0.91	0.10	0.30	33.39 ± 0.21	28.54 ± 0.45	8.45 ± 0.16	4.52 ± 0.32	4.08 ± 0.04	2.78 ± 0.15
Sep-17	4.37	166	38	0.88	0.96	0.16	0.18	31.93 ± 0.25	28.30 ± 0.41	7.07 ± 0.20	4.36 ± 0.30	4.22 ± 0.08	2.94 ± 0.23
Oct-17	2.36	33	14	0.59	0.75	0.38	0.75	31.87 ± 0.63	30.56 ± 1.01	7.39± 0.49	5.85 ± 0.72	3.90 ± 0.23	2.85 ± 0.17
Aug-18	6.50	13	2	0.68	0.74	0.13	0.02	32.54 ± 0.94	29.35 ± 0.15	7.76 ± 0.75	4.50 ± 0.50	4.38 ± 0.34	3.00 ± 1.00
Sep-18	4.00	40	10	0.96	0.91	0.03	0.21	31.30 ± 0.54	30.40 ± 0.85	6.70 ± 0.37	5.50 ± 0.70	4.20 ± 0.09	4.00 ± 0.49
Oct-18	0.73	22	30	0.87	0.86	0.10	0.43	30.56 ± 0.55	31.48 ± 0.55	6.22 ± 0.52	6.73 ± 0.46	4.31 ± 0.38	3.23 ± 0.09
Nov-18	1.80	9	5	0.85	0.89	0.06	0.10	32.08 ± 1.01	31.58 ± 1.63	7.66 ± 0.89	6.80 ± 1.59	3.66 ± 0.44	3.00 ± 0.00
Aug-19	2.00	12	6	0.81	0.82	0.08	0.04	31.87 ± 0.82	31.15 ± 0.60	7.08 ± 0.63	6.16 ± 0.47	4.25 ± 0.30	5.66 ± 1.05
Sep-19	14.00	42	3	0.97	0.94	0.03	0.22	32.07 ± 0.47	30.93 ± 1.30	7.28 ± 0.39	5.00 ± 1.00	4.80 ± 0.21	4.00 ± 0.00
Oct-19	1.37	26	19	0.91	0.94	0.23	0.02	32.31 ± 0.62	31.53 ± 0.57	7.09 ± 0.48	6.57 ± 0.42	4.61 ± 0.31	3.68 ± 0.27

Appendix H. Partial fullness index (PFI) of herring prey items that contributed more than 0.01% to the diet by weight. All prey items that contributed less than this threshold were collectively pooled as 'Other'. Total fullness index (TFI) is also presented as the total sum of all individual prey PFI values and conveys average stomach fullness by sampling period, standardized by herring total length. No sampling was conducted in November 2017 and 2019 (grey boxes).